Shorebirds in Marine Environments

FRANK A. PITELKA
Editor

Studies in Avian Biology No. 2

A PUBLICATION OF THE COOPER ORNITHOLOGICAL SOCIETY

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Cover Photographs: front, Sanderlings (*Calidris alba*); rear, Western Sandpipers (*Calidris mauri*); both taken on wintering grounds in central coastal California by Kenneth W. Gardiner.

STUDIES IN AVIAN BIOLOGY

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PREFACE

Early in 1976, George J. Divoky, then chairman of the Pacific Seabird Group, reported that the governing committee of the PSG had decided to sponsor a symposium on shorebirds at its next annual meeting, in January 1977. He invited me to organize it. I welcomed the opportunity for several reasons. First, I had attended the PSG's second annual meeting in December 1975 and found the program and its attendants to be a good mix of interests in research on marine birds. Attendance by representatives from federal and state agencies, both active field workers and administrators, was better than at most ornithological meetings. Moreover, the membership as a whole evinced a sense of mission with regard to environmental welfare of marine birds, reflecting the ongoing and prospective research on their ecology and conservation sponsored by government agencies. All this boded well for a program on shorebirds that would direct attention to matters of habitat critical for shorebirds as well as their basic biology.

Second, in the prior 20 years or so, research on basic ecology and behavior of shorebirds had advanced more rapidly on their breeding grounds than on migratory and wintering grounds, and some balancing of attention was clearly in order. This need was made all the more conspicuous by the simple fact that shorebirds spend 9–11 months on the latter, only 1–3 months on the former. A symposium reflecting current research interests on their nonbreeding areas could help to improve the balance.

Third, in view of the expanding front of research on shorebirds on the two sides of the north Atlantic, especially their migration patterns and winter habitat use, the time was clearly opportune for a review of parallel needs along the Pacific Coast. The western European community is well ahead for several reasons—its relatively compact geography, the numbers of active field observers, the magnitude ot their "ringing" programs, and the tradition of winter-season travel by ornithologists to southern Europe and Africa. By 1970, the surge of interest in shorebirds in Great Britain led to the organization of a Wader Study Group, with its own bulletin (no. 22 issued in August 1978). Along the Pacific Coast, by comparison, informational and manpower resources for research on shorebirds are limited, and to date, both geography (bear in mind distances on our long, linear coast) and politics appear to discourage the sort of international collaboration needed to address problems of habitat needs and migration patterns of shorebirds. Still, the Pacific Coast is not without some bright spots of accomplishments: The California Shorebirds Study, a cooperative program initiated with concern for preservation of wetland habitats and concluded in 1973 with a 275-page report, represents the only systematic and intensive use of shorebirds as indicators yet undertaken in the New World (see papers by Jurek and Speth). The Offshore Continental Shelf Environmental Assessment Program in Alaska, initiated in 1975 and for which the Bureau of Land Management is primary sponsor, represents a massive effort to provide baseline data and to assess prospective impact of coastal developments on biota generally, including shorebirds. A volcanic rush of new information is forthcoming. Questions of focus and follow-up for all this work remain, in California, Alaska, and elsewhere. It seemed clear that a symposium could help to bring all these matters into better perspective for both field workers and government agencies.

Accordingly, I sought papers on various aspects of shorebird biology and habitat conservation, which the contents of this volume illustrate well. By late summer, 1976, the developing program for the symposium spilled over the single day initially planned, and an extra half day was added. Time would not have allowed more papers than the contents of this volume. Yet initially, I did hope that more papers would result from my solicitations to Latin American workers and to representatives of government agencies responsible for coastal habitats in Oregon, Washington, British Columbia, and Alaska, but my success in these two respects was only modest.

With regard to Latin America, survey work of the sort illustrated by papers of Hughes (Perú) and of Smith and Stiles (Costa Rica) badly needs doing in other sectors of the Pacific Coast. Existing distributional information is still relatively rough, and data for a picture of relative abundance in species such as the Sanderling with immensely broad latitudinal distribution are scant or non-existent. Further, it appears that some discontinuities in coastal occurrence may reflect migratory landfalls or staging areas after or before long distance flights. A possible example is the Knot. It is important to try to identify these critical coastal sectors. Still further, more primary work as well as a summary for the occurrence of nonbreeders during the boreal summer are needed for tropical and austral coasts. The paper by Johnson for nonbreeders on a Pacific atoll suggests problems of interest beyond mere distribution. A coordinated program for year-round censusing of selected sectors spaced along the Pacific Coast from San Diego to Tierra del Fuego would serve as an essential foundation for more sophisticated work on shorebird biology as well as on assessment and conservation of coastal habitats.

With regard to the North American coast north of California, the greatest amount of work is of course going on in Alaska, illustrated here by four papers. I had hoped to get a more general paper reviewing problems of coastal habitat classification and preservation as seen in these critical times for that state. This seemed like a reasonable hope considering the years and vast numbers of man-hours spent, by both federal and state agencies, in field work and in the yo-yoing of small planes in reconnaissance work along all sectors of the coast. But I failed. It appeared that in Alaska, in 1976, the multi-level political stir brought on by the whole bag of oil-related problems, with cumbersome bureaucracies facing conditions changing at a dismaying pace, was such that no one would or could face the job of broad synthesis about coastal habitats from the shorebird standpoint, even though the basic information exists. Perhaps this symposium will help to focus on a need whose importance is clearly and strongly suggested by papers here of Senner, Isleib, and Gill and Jorgensen.

Finally, and more generally, the PSG's shorebird symposium, like other symposia focusing on particular problems, taxa, and geographies, should help to improve the direction and pace of research in an area of active interest. Various results reported here call for additional work of potential significance at both basic and applicational levels, for example, the phenomena of site tenacity (Kelly and Cogswell) and dependence of wintering shorebirds on mosaic patterns of habitats (Page et al., and Gerstenberg). Also summaries of work on the British front by Prater and Goss-Custard help to chart directions for future work on the Pacific Coast. The reader will discern more than is mentioned here, and will judge all. The fact that remains is that the continuing interplay between basic studies of shorebird biology and their use in coastal wetland assessment and conservation should keep the front of research moving significantly.

ACKNOWLEDGMENTS

I thank many colleagues and friends for significant help in this venture. Those I can remember and have to mention especially include George J. Divoky and the Pacific Seabird Group for creating the occasion for a shorebird symposium and for their warm support throughout; L. Richard Mewaldt, local program chairman for the 1977 meeting at Asilomar, and his staff for generous and efficient help in planning and running of the meeting itself; M. R. Foster, T. R. Howell, J. R. Jehl, Jr., and O. P. Pearson for advice on Latin American activities in shorebird work; C. Hand, J. D. Cubit, J. W. Hedgpeth, and W. J. North for help with background information useful for my introductory paper in particular as well as the symposium in general; Peter C. Lent and the BLM-NOAA offices in Boulder, Colorado, for travel support of speakers from Great Britain; Daniel W. Anderson and the PSG's publication committee for counsel on planning the symposium for publication; Ralph J. Raitt, editor for Studies in Avian Biology, for guidance and assistance in readying manuscripts for the printer; J. P. Myers for listening to me and giving useful reactions at all stages of this symposium; and last but definitely not least, the Fish and Wildlife Service and its Deputy Associate Director, Harvey K. Nelson, for support of the Pacific Seabird Group through a grant contributing significantly to the cost of publication.

Frank A. Pitelka

September, 1978

Studies in Avian Biology No. 2:1–11, 1979.

INTRODUCTION: THE PACIFIC COAST SHOREBIRD SCENE

FRANK A. PITELKA[1]

Let me begin by welcoming you all to the Pacific Seabird Group meeting, of which the first part is a shorebird symposium that will occupy this afternoon and all day tomorrow [6–7 January 1977]. The more formal opening of the PSG meeting will be handled tomorrow morning, by Chairman George Divoky and other officers of the organization. I am the first speaker on the symposium and will offer you some introductory comments which I hope will be useful in our thinking about the presentations that follow.

But before that, let me give you what I think are the objectives of this symposium. There are two, and they interlock critically. First, we are looking at current work on the distribution, migration and ecology of shorebirds in marine and coastal environments from the standpoint of basic information and the moving front of knowledge about them. Second, we are also looking at these topics from the standpoint of conservation and management of coastal wetlands that are important to the welfare of shorebirds and, indeed, of all other maritime birds as well. In particular, how can shorebird-habitat interrelationships sharpen our sense of responsibility toward habitat—that is, how can shorebirds help us to assess, select and preserve coastal wetlands? Attending our meeting are representatives of federal and state agencies, and it is a particularly strong desire on the part of all of us who have been involved in getting this symposium organized to emphasize this applied side of our symposium subject. The papers following mine will be addressing themselves to our two objectives, singly or in combination.

For my introductory comments, I have chosen to look at shorebird biology and distribution along the Pacific Coast from a fairly global point of view. Such a view is forced upon us when, for example, we think about the relative importance of different sectors of the coast and the degree to which they must figure in any efforts to select and preserve coastal wetlands that will be not only representative, but also really adequate. After all, shorebirds are long-distance migrants, and this larger view of the coast as an eco-geographic system is necessary and, indeed, inescapable for an understanding of shorebird migrational dynamics and the habitats they need to complete their annual cycles. In the remaining time, for me to pursue that idea seriously would be to presume that we have all sorts of information available, which, as we sadly must admit, is for the most part not true. Nevertheless, this global view is the background for the two parts of my talk: First, I will summarize shorebird distributions along the entire Pacific Coast, and second, I will discuss briefly several biological and geographic factors that figure in that global view.

First, let us look at the world shorebird fauna in order to extract from it the fraction occurring on the Pacific Coast. In Figure 1 are listed the six charadrioid families with species totals. The New World shorebirds consist of four groups—those that are strictly New World (52 species), those that spill over additionally into Asia (5 species), those that are Holarctic (11 species), and those that are Old World *and* spill over additionally into North America (3 species). The total is 71 species (Table 1), of which 57 or 80% are maritime—that is, they figure in the

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TABLE 1

NEW WORLD SHOREBIRDS[a]

KEY TO SYMBOLS:	A	Asiatic breeding in Alaska	Non-m	Non-maritime (absent from maritime habitats)
	b	Breeding	Non-PC	Non-Pacific Coast
	H	Holarctic	PC	Pacific Coast
	NA	North American	SA	South American
	NA-A	North American spilling into Asia	SH	Southern hemisphere
	NH	Northern hemisphere	T	Transequatorial
	Non-b	Non-breeding	w	Western
	Non-c	Non-coastal (absent from coastal lowlands)		

Family	Distributional class[b]	Genus and Species	Vernacular name	Comments
ROSTRATULIDAE	SA	*Nycticryphyes semi-collaris*	Painted Snipe	Resident
HAEMATOPODIDAE		*Haematopus palliatus,*	American oystercatcher	Resident
	T	including *H. p. bachmani*	North American Black Oystercatcher	Resident
	SA	*H. leucopodus*	Magellanic Oystercatcher	Resident
	SA	*H. ater*	South American Black Oystercatcher	Resident
CHARADRIIDAE	SA	*Vanellus chilensis*	Southern Lapwing	Only local movements
		Vanellus resplendens	Andean Lapwing	Non-c
		Hoploxypterus cayanus	Pied Plover	Non-PC
	NA	*Pluvialis squatarola*	Black-bellied Plover	Migrant
	H	*Pluvialis dominica*	American Golden Plover	In non-b seasons, rare to casual on PC
		Charadrius hiaticula	Ringed Plover	Non-PC
	NA	*C. semipalmatus*	Semipalmated Plover	Migrant
		C. melodus	Piping Plover	Non-PC
	T	*C. alexandrinus*	Snowy Plover	Weakly migrant in NH; resident in SH
	SA	*C. falklandicus*	Two-banded Plover	Weakly migrant
		C. alticola	Puna Plover	Non-c
	T	*C. collaris*	Collared Plover	Resident
	T	*C. vociferus*	Killdeer	Migrant; SH race resident
	T	*C. wilsonia*	Wilson's Plover	Resident
		C. montanus	Mountain Plover	Non-c
		Oreopholus ruficollis	Tawny-throated Dotterel	Non-m

TABLE 1. (CONTINUED)

Family	Distributional class^b	Genus and Species	Vernacular name	Comments
	SA	*Zonibyx modestus*	Rufous-chested Dotterel	Migrant
		Pluvianellus socialis	Magellanic Plover	Non-PC; only local movements
		Phegornis mitchelli	Diademed Sandpiper-plover	Non-c
SCOLOPACIDAE				
Tringinae		*Bartramia longicauda*	Upland Sandpiper	Non-m
		Numenius borealis	Eskimo Curlew	Probably extinct (or = *N. minuta*)
	H	*Numenius phaeopus*	Whimbrel	Migrant
	NA	*N. tahitiensis*	Bristle-thighed Curlew	Migrant; winters on Pacific islands
	NA	*N. americanus*	Long-billed Curlew	Migrant; b non-m
	NA	*Limosa haemastica*	Hudsonian Godwit	Migrant; not along NA PC
	A	*L. lapponica*	Bar-tailed Godwit	Migrant thru Aleutians; winters in SW Pacific region
	NA	*L. fedoa*	Marbled Godwit	Migrant; b non-m
	NA	*Tringa flavipes*	Lesser Yellowlegs	Migrant; b non-m
	NA	*T. melanoleuca*	Greater Yellowlegs	Migrant; b non-m
		T. solitaria	Solitary Sandpiper	Non-m; inland migrant
	NA	*Actitis macularia*	Spotted Sandpiper	Migrant; b non-m
	NA	*Catoptrophorus semipalmatus*	Willet	Migrant; b non-m
	NA	*Heteroscelus incanus*	Wandering Tattler	Migrant; also winters on Pacific islands
Arenariinae	H	*Arenaria interpres*	Ruddy Turnstone	Migrant
	NA	*A. melanocephala*	Black Turnstone	Migrant
Scolopacinae	NA-A	*Limnodromus scolopaceus*	Long-billed Dowitcher	Migrant; chiefly non-m
	NA	*L. griseus*	Short-billed Dowitcher	Migrant
	H	*Capella gallinago*	Common Snipe	Migrant
	SA	*C. paraguaiae*	South American Snipe	Resident; southernmost population migrates
		C. nobilis	Noble Snipe	Non-c
		C. undulata	Giant Snipe	Non-c
		Chubbia imperialis	Bogota Snipe	Non-c (Bogota, Col.; rare)
		C. Jamesoni	Andean Snipe	Non-c
		C. stricklandi	Cordilleran Snipe	Non-c
		Philohela minor	American Woodcock	Non-m

TABLE 1. (CONTINUED)

Family	Distributional class[b]	Genus and Species	Vernacular name	Comments
Calidridinae	NA	*Aphriza virgata*	Surfbird	Migrant
	H	*Calidris canutus*	Red Knot	Migrant; uncommon on w SA coast
	H	*C. alba*	Sanderling	Migrant
	NA	*C. pusillus*	Semipalmated Sandpiper	Migrant; not along NA PC
	NA-A	*C. mauri*	Western Sandpiper	Migrant
	A	*C. ruficollis*	Rufous-necked Sandpiper	Migrant; winters in SE Asia and Australia
	NA	*C. minutilla*	Least Sandpiper	Migrant
	NA	*C. fuscicollis*	White-rumped Sandpiper	Migrant; not along NA PC
	NA-A	*C. bairdi*	Baird's Sandpiper	Migrant; occurs on PC in SA
	NA-A	*C. melanotos*	Pectoral Sandpiper	Migrant; rare along NA PC
		C. maritima	Purple Sandpiper	Non-PC
	NA-A	*C. ptilocnemis*	Rock Sandpiper	Migrant
	H	*C. alpina*	Dunlin	Migrant
	A	*C. ferruginea*	Curlew Sandpiper	Migrant; breeds in northern Alaska; winters in Old World SH
		Micropalama himantopus	Stilt Sandpiper	Non-PC
	NA	*Tryngites subruficollis*	Buff-breasted Sandpiper	Non-PC except arctic Alaska; non-m on wintering range
RECURVIROSTRIDAE	T	*Himantopus mexicanus*	Black-necked Stilt	Migrant; northern SA population resident
	NA	*Recurvirostra americana*	American Avocet	Migrant
		R. andina	Andean Avocet	Non-c; resident
PHALAROPODIDAE	H	*Phalaropus fulicarius*	Red Phalarope	Migrant
	H	*Lobipes lobatus*	Northern Phalarope	Migrant
	NA	*Steganopus tricolor*	Wilson's Phalarope	Migrant; b non-m

[a] Limited to the super family Charadrioidea; taxonomy based on Peters (1934) and Hellmayr and Conover (1948) revised to agree with the A. O. U. check-list (1957) and its supplements; distributional data drawn from these sources and from de Schauensee (1964), Friedmann et al. (1950), Gabrielson and Jewett (1940), Gabrielson and Lincoln (1959), Grinnell and Miller (1944), Humphrey et al. (1970), Jehl and Rumboll (1976), Jewett et al. (1953), Johnson and Goodall (1965), Land (1970), Olrog (1968), Salo (1975), Saunders et al. (1950), and Wetmore (1965).

[b] Species assigned to distributional classes are those entering into compilations for Figures 3 and 4. All others are dismissed under 'Comments' as not occurring on or near the Pacific Coast (non-PC), or if present on Pacific drainage slopes at whatever elevations, they are non-coastal (non-c), or if coastal, they are non-maritime (non-m). Note that some species occurring along the Pacific Coast as migrants and winter residents breed inland (b non-m), to distinguish them from species which utilize maritime (and inland) habitats during the breeding season.

WORLD SHOREBIRD FAUNA

	OLD WORLD ⟶	and Alaska	BOTH	and Siberia	⟵ NEW WORLD	TOTALS
Rostratulidae Painted Snipe	1				1	2
Haematopodidae Oyster catchers	2				3	5
Charadriidae Plovers	44		2		17	63
Scolopacidae Sandpipers	41	3	7	5	27	83
Recurvirostridae Avocets, etc.	5				3	8
Phalaropodidae Phalaropes			2		1	3
	93	3	11	5	52	164
	112		71			
MARITIME	?		57 (80%)			

FIGURE 1. An analysis of the world shorebird fauna (superfamily Charadrioidea) giving species totals by family subdivided according to New World and Old World occurrences. The New World total is 71 species of which 19 are shared with the Old World, and of which 57 (or 80 percent) utilize maritime habitats in any phase of their annual cycles.

ecology of coastal wetlands, many importantly, some negligibly. Of these 57, however, only 49 occur on or near the Pacific Coast. We reduce that figure by four species (three Asiatic species in Table 1 plus *Numenius tahitiensis*) breeding in northern latitudes of America, but taking off for Asia and the Pacific islands in migration, so that only 45 occur along the Pacific Coast south of the Alaska Peninsula. Of these, 33 are North American breeders, six are trans-equatorial, and six are South American. There is some play in these figures due mainly to the fact that information for Central and South America is poor.

In order to reduce details of distribution to a graphic, compact picture, I divided the Pacific Coast into 5-degree latitudinal belts (Fig. 2) and plotted occurrences in these belts. For purposes of this analysis, the Pacific Coast is the entire coastline from Cape Horn up to and beyond Bering Strait to Point Barrow. By this extention to Point Barrow, we manage to include a fraction of the breeding range (and exclude none) of high arctic species that occur along Pacific Coast.

The species occurrences by 5-degree belts during the boreal or northern summer are shown in Figure 3. Species density is strikingly high in the northern latitudes, reaching a peak of 28 in the 60–65° interval, which is the belt roughly running from Seward Peninsula down to the Kuskokwim River. The breeding occurrences of North American species fall off rapidly southward. We then pick

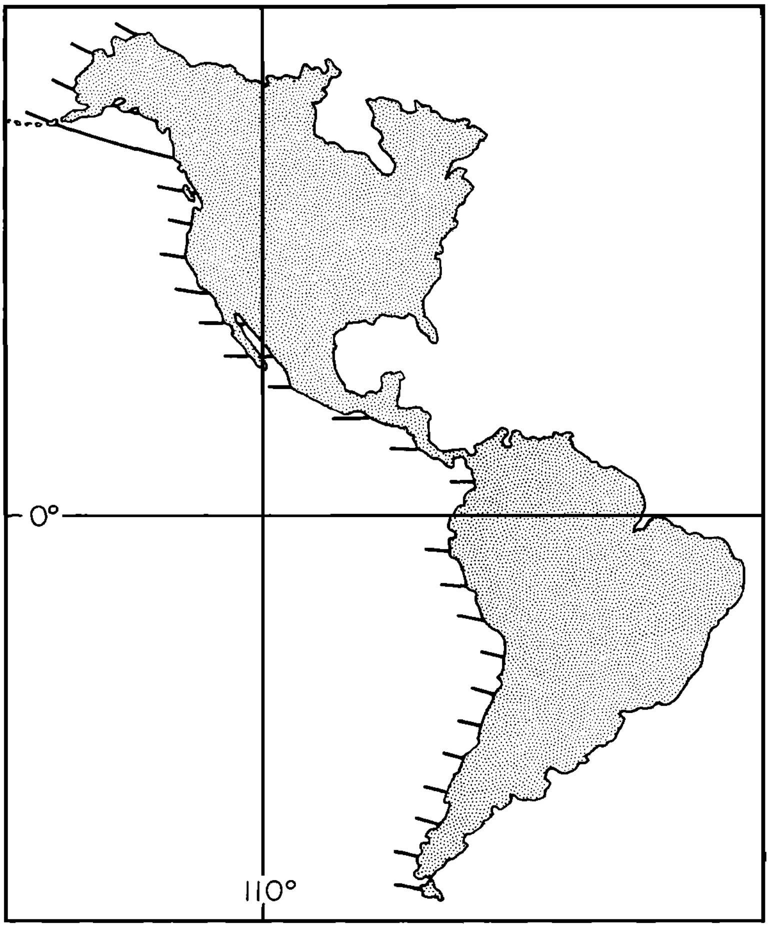

FIGURE 2. The New World showing five-degree intervals along the Pacific Coast used in plotting species densities shown in Figures 3 and 4.

up a trans-equatorial group that occurs through a wide belt, the species most notorious in this respect being the Oystercatcher. Number of species in this group is low, there being only four or five through a 30° belt halved by the equator. And finally we have a small group of South American species, which, with several of the more southern trans-equatorial species, reach a maximum number of nine in the 40–45° interval.

A datum missing from Figure 3 is the number of northern species represented by non-breeding individuals that remain at mid- or southern latitudes through the austral winter (see beyond). The significance of this phenomenon varies from species to species; for some, non-breeding occurrence of first-year individuals at southern, "wintering" latitudes is apparently a regular feature of their annual cycle. But the available distributional data are not only scant, they are too scattered for me to attempt to add the non-breeder component to Figure 3 at this time. But the phenomenon deserves attention, and a synthesis of existing data, limited though they are now, would be worthwhile. [See Bullock 1949 and Eisenmann 1951 for earlier notice of this phenomenon.]

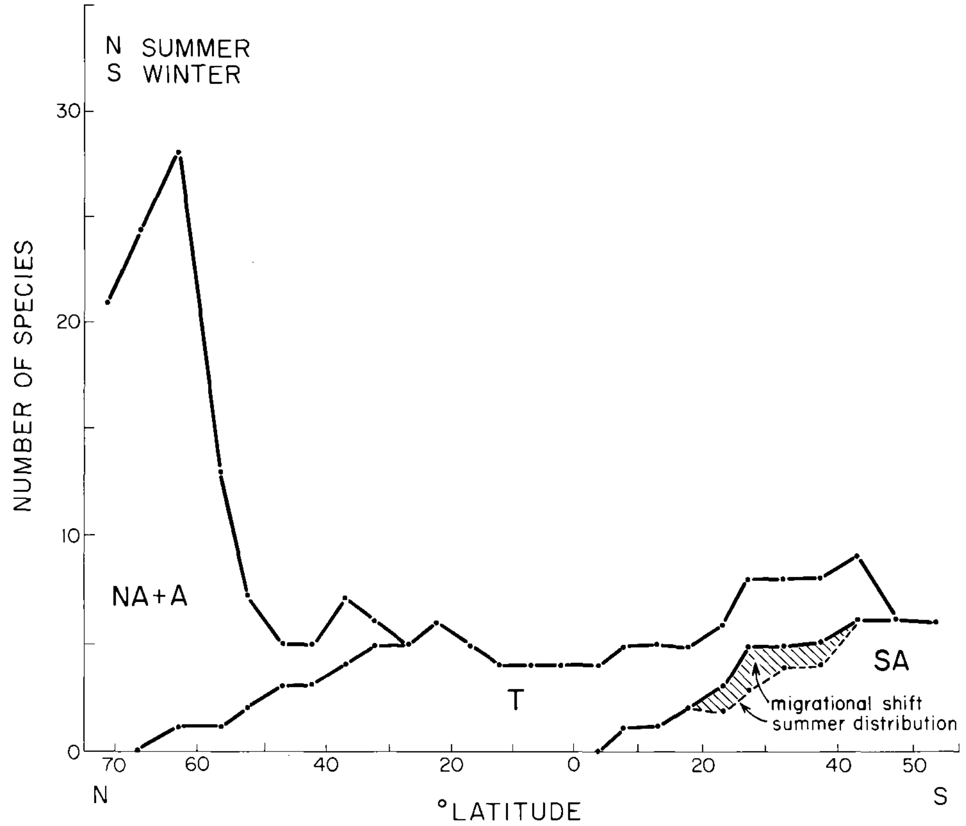

FIGURE 3. The occurrence by five-degree intervals of shorebird species totals during the northern summer (southern winter), subdivided into North American plus Asiatic (NA + A), transequatorial (T), and South American (SA). See text for further explanation.

The distribution of the South American group is shown in Figure 3 for both the southern or austral winter and the southern summer. This brings out the relatively small amount of latitudinal shift of these southern species from a migrational standpoint. The available information on this matter is scant, of course, but the fact remains that migrational distances among these southern species are piddling compared to what we will see it is for the northern species. [However, J. P. Myers tells me that "southern species *pile* into central Argentina during the nonbreeding season. This shift is significant."]

The picture in the southern or austral summer is given in Figure 4. As in Figure 3, the numbers in the distributional classes in each latitudinal belt are graphed cumulatively (except for the dashed line; see below). Again, note the summering South American species, the trans-equatorial species, and now the North American species as they spread themselves over Middle and South American latitudes during their 'wintering' residency. Superimposed on this are occurrences in successive 5-degree belts that are strictly transit occurrences of species between their breeding and wintering ranges. For comparison, the boreal summer distributions of North American species are shown by the dashed line.

Two striking things come out of Figure 4: First, the shorebird fauna of South

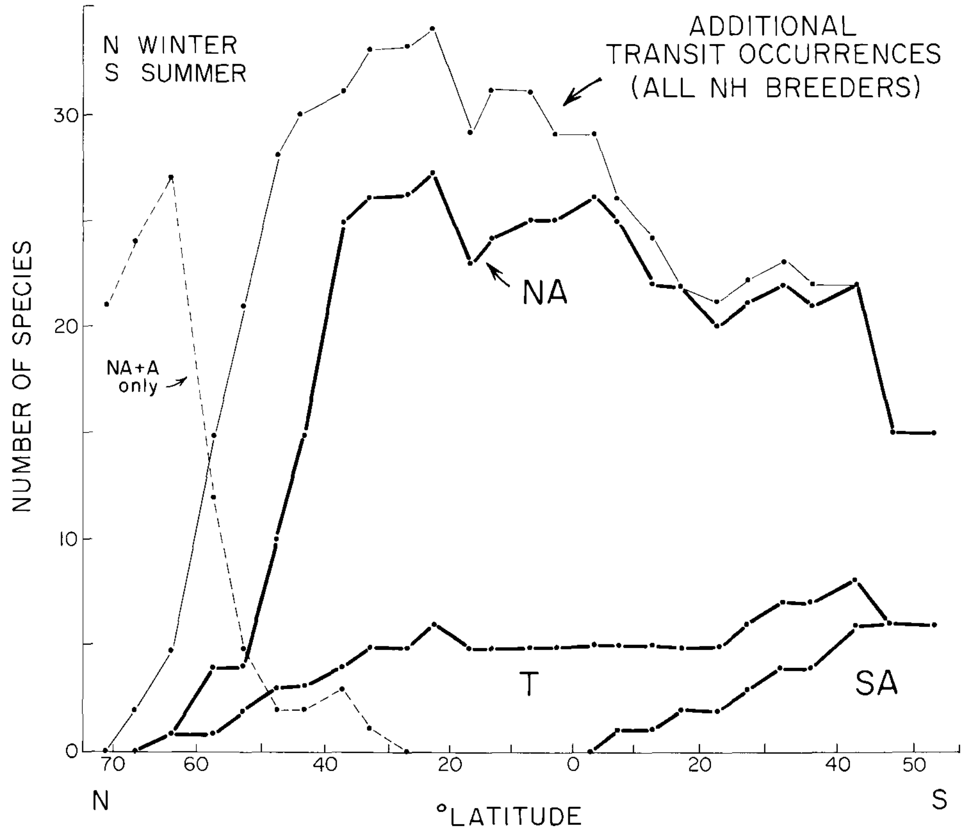

FIGURE 4. The occurrence by five-degree intervals of shorebird species totals during the northern winter (southern summer) subdivided as in Figure 3. Additional occurrences by five-degree interval of species found in each as migrants are also shown. For comparison, totals for North American species during the northern summer are shown by a broken line. See text for further explanation.

America is roughly quadrupled by the influx of North American migrants, and second, the northern species winter in highest species density between 40°N (near Cape Mendocino, northern California) and 40°S (near Valdivia, southern Chile). A fascinating thing about this picture is the degree to which the North American species, heavily concentrated in their breeding distribution, spread out over an enormous latitudinal sector of the bi-hemispheric coastline. Along the Pacific, and in similar manner though of course not in detail along other bi-hemispheric coastlines, the distributions are not continuous, but the significance of discontinuities is almost impossible to assess now on the Pacific Coast due to lack of data on relative abundances along successive sectors of the coast.

Such, briefly, is the distributional picture for shorebirds on the Pacific Coast, and I turn now to several factors that contribute significantly to the need to view the ecology and conservation of shorebirds along a coast such as the Pacific as an eco-geographic system. There is, first of all, the business of staging areas. By 'staging area' I refer to a site where migrating shorebirds ready themselves physiologically for the next migrational leap. We are acutely aware of the importance of staging areas in the latter part of the spring migration, in northern parts of migrational routes, but this does not mean that staging areas may not be important also to the south of the political limits that now tend to confine us in our thinking about the matter. There are some puzzling gaps in the known occurrences of several species along the Pacific Coast that clearly suggest landfall and staging areas of as yet unknown location and importance in Central America and more southern latitudes.

Second, there is the business of tightness of migrational movement. Spring migration is tight in the sense that it is limited temporally more strongly than it is in the fall, and so one might think that staging areas are more important in the spring than they are in the fall. And yet the apparent looseness of fall timing may just be an artefact in our existing information about fall movements. In the first place, there are age differences in the fall; that is, age groups tend to sort out temporally in interesting and critical ways when we have the information. Therefore, the pacing of migration, the occurrence of staging areas, and the intervals between staging areas may be of importance to our knowledge of shoreline habitat in the fall as it is in the spring. Not only that, but the very fact of molt schedule tied to fall migration and to arrival on wintering grounds suggests that there may be critical aspects to the timing of fall migration that we are only now beginning to sense.

Third, there is the evidence from an increasing number of species that wintering populations stay put and return to the same area. This wintering site tenacity again says that with regard to timing of arrival on wintering grounds, and with regard to period of residence there and exploitation of whatever resources are necessary not only to survive, but to molt and prepare for spring migration, we need to improve our knowledge of critical shoreline habitat. This becomes both complicated and urgent because of differences in habitat needs among different species and because of the constraints imposed on the process of identifying and assessing important habitat when the supply is already so limited, at least at heavily populated temperate latitudes.

Fourth, there is variation in sex ratio among populations of one species in different latitudinal sectors of a coastal distribution. We know such between-population differences occur, for example, in many species of ducks, but at the moment, I am not aware of any shorebird species for which we have good data. In the latest issue of Bird-Banding, there is an interesting report of a sampling of Least Sandpipers in Surinam (Spaans 1976) that yielded a sex ratio of 6 females to 1 male. The sample was small, but it is suggestive, and indeed we should expect that latitudinal differences in sex ratio will occur in wintering populations of shorebirds. Again, this has implications with regard to habitat needs of shorebirds. [At the symposium, A. J. Prater commented on evidence of heavily female-weighted sex ratios in the Ruff, *Philomachus pugnax,* in south Africa. For data, see Greenhalgh 1968, Pearson et al. 1970, and Schmidt and Whitehouse 1976. Also, J. V. Remsen has called my attention to data on unequal sex ratios in the Dunlin (Page 1974) and Western Sandpiper (Page et al. 1972).]

There are still other features of shorebird distribution worth noting in this vein—for example, the non-breeding fractions of populations that remain on their wintering or migrational grounds, or the spillover from the Caribbean into the Pacific Coast system at Panamanian latitudes of such species as the American

Golden Plover and Semipalmated Sandpiper. But time is too short to go into any detail.

Finally, I want to mention a couple of geographic factors. Compared to the Atlantic Coast, the Pacific is straighter, and this means that it has considerably fewer miles of shoreline available to shorebirds. Furthermore, it is also climatically less favorable, the most obvious feature in this respect being the desert latitudes—the northern Mexican stretch and the Peruvian-northern Chilean stretch. A more general way of making this point is to observe that there is significantly less flow of fresh water into the Pacific than into the Atlantic, and this means that other things being equal (which they are not, viz. topography), there will be, and is, proportionally less coastal wetland habitat. Beyond the desert latitudes, this problem is most serious in the adjacent Mediterranean latitudes where rainfall can be severely limited, as we are now well aware in California [in 1975–76 and 1976–77]. The consequence of these geographic considerations is that the relative importance of different coastal sectors from the standpoint of shorebird habitat needs is going to vary more critically along the Pacific than it does along the Atlantic. And this means that it becomes more urgent to look at the significance of different sectors of the coast with regard to the welfare of species populations that comprise the fauna.

Another geographic factor is that of tides. I have been mucking around in the intertidal for years, from the subtropics to the arctic, and one impression I have gained is that notwithstanding local factors, there is a general trend from the equator to higher latitudes (although not beyond Bering Strait) of increasing amplitude in the tides. There are of course local complications—form of the coastline, depth and bottom topography of adjacent ocean, and other proximate factors as well as more remote ones such as the long-term cycle of the moon. We have checked tidal amplitudes at different times of the year from Barrow to Cape Horn taking stations at more or less 10-degree intervals of latitude, and in fact, this trend appears to be real. The funny thing is that to date I have not been able to check the matter satisfactorily. I cannot find any consideration of it in the literature notwithstanding the heaps of data from numerous stations of predicted intervals and timing of tides. The actual study of tidal dynamics has progressed most strongly in western Europe, where the scope for latitudinal comparison is of course limited. And other than a few large-scale maps of co-tidal lines in the two main ocean masses, there is nothing of a general, synthetic character that assists us in getting down to the sort of question I am posing for the Pacific Coast as a whole. We have already noted that overall, migrating shorebirds face more variable, more unpredictable conditions on the Pacific Coast than on the Atlantic where climates are wetter and coastal wetlands more extensive. If this is so, the factor of clinal narrowing of tidal amplitude toward the equator augments this contrast, narrowing area of potentially usable intertidal habitats and thus exacerbating questions of critical habitat needs for migrating shorebirds. A prediction one could make from these considerations is that the overall relative incidence of shorebirds occurring as non-breeders on wintering and migrational grounds may be higher on the Pacific than on the Atlantic.

This concludes very quickly—and I'm sorry how necessarily quickly—what I have to say. In these remarks I am anticipating things that will be developed further by the speakers, but my main message to you is that we need to work at acquiring a better sense of system in studying shorebirds in coastal wetlands. Along the Pacific this calls for some sort of systematic monitoring on a grander scale than any attempted to date, going beyond political limits that have confined us to date. We need to think and work on a more global scale.

ACKNOWLEDGMENTS

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PART 1:

DISTRIBUTION, MIGRATION, AND CONSERVATION

Studies in Avian Biology No. 2:15–32, 1979.

ASPECTS OF THE OCCURRENCE OF SHOREBIRDS ON A CENTRAL CALIFORNIA ESTUARY

GARY W. PAGE, LYNNE E. STENZEL, AND CLAIRE M. WOLFE[1]

ABSTRACT.—All shorebirds on Bolinas Lagoon in central California were censused every other five-day period from June 1971 to May 1976. These censuses, together with observations of molting birds, revealed that shorebird occurrence on Bolinas Lagoon fits four general patterns: (1) occurring only during fall migration, departing prior to the prebasic molt, and usually occurring again during spring migration; (2) arriving early in fall, undergoing prebasic molt, and wintering; (3) arriving late in the fall after the prebasic molt is mostly completed and overwintering; and (4) breeding, overwintering, and probably molting on Bolinas Lagoon. In densities, smaller species outnumbered larger species but contributed less to total shorebird biomass on the estuary. Considerable annual variation in numbers was observed in some species but not in others.

Censuses of salt marsh and tidal flat habitats revealed considerable variation among species in use of different areas within Bolinas Lagoon. The salt marsh was most important as a roosting area although a few species also fed there. Most species used the tidal flat as their main feeding area. Different species segregated onto tidal flats of different substrate types, and tidal flats of intermediate substrate texture supported the highest densities and widest variety of birds. Extralimital habitats, such as open coast adjacent to Bolinas Lagoon and pastureland on the Bolinas mesa, were also used by certain shorebirds indicating the importance of habitats outside the estuary in support of local shorebird populations. Comparisons of shorebird densities between Bolinas Lagoon and Limantour Estero revealed that densities for given species often varied considerably between estuaries only a few kilometers apart. Some of this variation appeared to be due to obvious habitat differences, but often the variation could not be explained.

Some problems of interpreting shorebird census data are discussed, and factors affecting numbers and kinds of shorebirds occurring in coastal wetlands are mentioned. It is suggested that, due to variability in densities of shorebirds supported by different wetland habitats, destruction of an entire system or even a part of one may result in habitat loss for some species that may not be compensated for by remaining habitat. An example is presented illustrating that some wetland areas do not support wintering shorebirds independently but, instead, as parts of larger integrated wetland systems.

Conservation and management of California's remaining coastal wetlands requires an understanding of the variation in the numbers and kinds of wildlife supported by different wetland areas. This understanding should begin with a knowledge of the relative abundance throughout the year of each species using each area, the amount of natural variation that can be expected between different years in numbers, and the ways areas differ in meeting the needs of each species. Several studies based on censuses of birds in coastal wetland habitat have generated a good deal of information on the number of birds using specific areas during different times of the year, and when looked at together provide valuable information on the importance of different coastal areas to many species (Storer 1951, Smail and Lenna 1969, Bollman et al. 1970, Gerdes 1970, Gerstenberg 1972, Gill 1972, Jurek 1973). The interpretations that can be made from these studies are limited, however, because in most cases censuses were only conducted for one year and because most study sites were part of larger wetland areas, making it difficult to distinguish between fluctuations in the numbers of birds at the study sites caused by local movements of the birds and fluctuations caused by changes in seasonal abundance.

Between 1971 and 1976 we regularly censused shorebirds on Bolinas Lagoon, an estuary at the south end of Point Reyes National Seashore in California.

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[1] Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970.

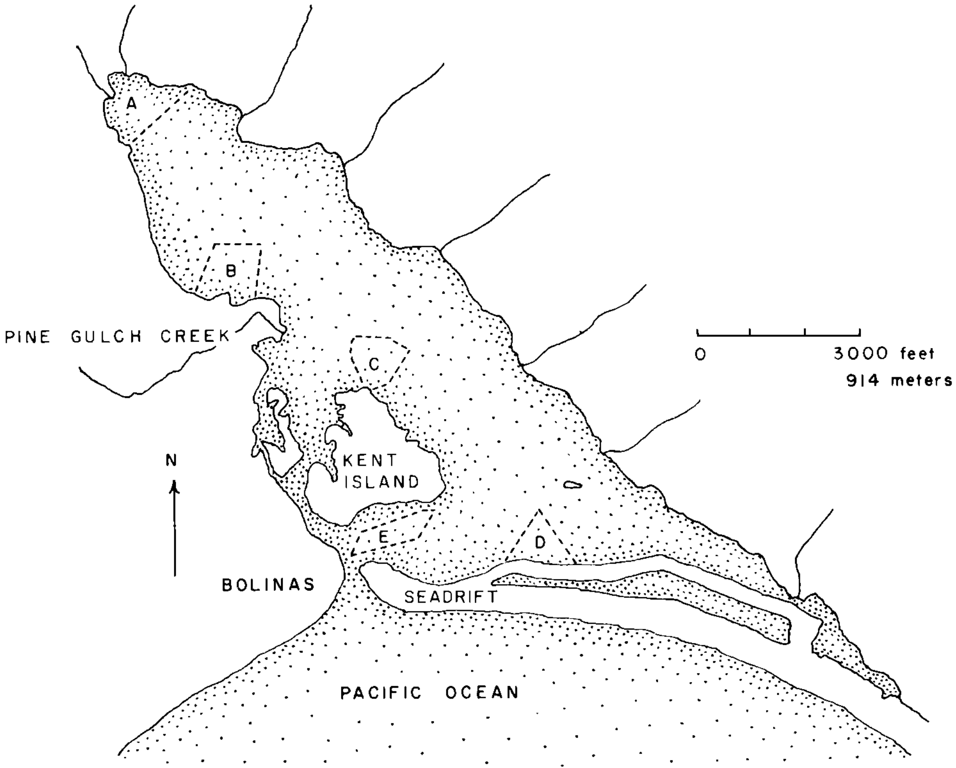

FIGURE 1. Sketch of Bolinas Lagoon. Areas A (12.6 ha), B (9.8 ha), C (8.0 ha), D (7.0 ha), and E (8.4 ha) are the five areas of tidal flat censused.

Several features of Bolinas Lagoon allowed us to obtain more precise census data than has been possible in most other shorebird census studies and, therefore, to make some interpretations different from those made in other studies. Bolinas Lagoon is small enough to be censused by three parties in three hours yet large enough to regularly hold from 3000 to 7000 shorebirds of at least 18 species. It is relatively isolated from other wetlands so that, for most species, census results do not reflect large fluctuations due to local movements of the birds. Finally, Bolinas Lagoon was quarantined against human use throughout the study and, consequently, received minimal human disturbance. We were able to graph the seasonal abundance patterns for most species, to compare the annual abundance over five years for each species, to examine variation in shorebird densities and biomass between different sub-areas of Bolinas Lagoon, and to compare bird densities between Bolinas Lagoon and Limantour Estero, a nearby estuary.

STUDY AREA AND METHODS

Bolinas Lagoon is a small shallow estuary 24 km northwest of San Francisco, California. High hills, marshy pastures and the Seadrift sand spit surround this wedge-shaped estuary except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into it year round and is the main source of the estuary's fresh water. Kent Island is a 40-ha island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species are *Salicornia virginica* and *Spartina foliosa*. At mean low water about 70% of Bolinas Lagoon comprises tidal flats which are divided by several channels (Ritter 1969).

We censused all shorebirds on Bolinas Lagoon during alternate five-day periods, except in June some years, from June 1971 to May 1976. Censuses were taken on rising tides, or falling tides if rising tides were not available, at 1.1–1.7 m above mean low water. During a census the estuary was divided into three areas and a team of observers in each area counted or estimated all shorebirds in that area. The counts in the areas were made simultaneously. Dowitchers were not identified to species on censuses but were sometimes identified between censuses. Some censuses included numbers of small sandpipers that could not be separately identified as Dunlin (*Calidris alpina*), Least Sandpiper (*Calidris minutilla*), or Western Sandpiper (*Calidris mauri*) but on no census did such observations exceed 20% of the identified small sandpipers. The unidentified sandpipers were incorporated into a census total as Dunlins, Least Sandpipers, and Western Sandpipers according to the relative abundance of firm identifications of these species on the census. Sometimes we counted rare or uncommon species prior or subsequent to a census, but within the five-day census period, because these birds were easily overlooked on the regular census. Because Snowy Plovers (*Charadrius alexandrinus*) are present year round but are difficult to find when their roosting area has been disturbed, we ignored zero values for this species in all calculations.

Additional censuses of specific areas on or near Bolinas Lagoon were also made to find out which were most used by the birds. During 1973 and 1974 we censused shorebirds in the salt marsh on Kent Island at low and moderate tides several times a month and on 8.5 km of open coast (comprising sand to pebble beaches and soft shale reef) adjacent to and north of Bolinas Lagoon three times a month. During the winters of 1972–73 and 1973–74 at high tide we frequently censused shorebirds on closely-cropped pastures about 2 km west of Bolinas Lagoon.

We selected five areas within the tidal flat of the estuary (Fig. 1) for intensive censusing in 1973 and 1974. The substrate of area A was very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris such as twigs and leaves. Much of the high-water zone of this area was covered by a layer of sediment which dried and cracked into leathery plates when exposed to air for long periods. The high-water zone abutted a small salt marsh through which a freshwater stream ran year round; the low-water zone bordered a basin. Area B was similar to area A except that a freshwater stream ran into it only during periods of heavy rain and the substrate ranged from fine to medium sand (Ritter 1969). The substrate of area C was a well to moderately sorted fine sand (Ritter 1969) and lacked the terrestrially derived organic debris of areas A and B. Unlike areas A and B the high-water zone of area C was pock-marked with the burrow openings of the ghost shrimp (*Callianassa californiensis*) and was not covered by hard dried plates of sediment. The high-water zone of area C abutted the Kent Island salt marsh on one side and a channel on the other; the low-water zone bordered a small basin. Area D had a substrate of moderately sorted fine sand (Ritter 1969) and was bordered on two sides by channels and on a third by a basin. The high-water zone in the center was less burrowed than area C. Area E differed markedly from the other areas. It comprised sediment ranging from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low-water zone. The high-water zone was separated from the Kent Island sand beach by a shallow channel; the low-water zone bordered a main channel.

In each of the five areas 10 censuses in which feeding and non-feeding birds were counted were made each month during the 1973–74 season. Each month we tried to census on all combinations of high, moderate, and low water with ebb tides, flood tides and slack water. We tried to take censuses for a particular tidal condition in all areas on the same day.

To fit our census data with the shorebird's annual cycles we defined one "season" as lasting from June to the end of May the following year. A fall period is defined as July through October; a winter period as November through February; a spring period as March through May; and a summer period as the month of June. The fall period, characterized by relatively warm dry weather at Bolinas, is when most of the autumn shorebird migration occurs. The winter period normally corresponds with most of the rainy weather and a minimal amount of shorebird migration compared to fall and spring. The spring period heralds the return of warmer, drier weather to Bolinas and encompasses most of spring migration. During June most shorebirds have left the area for breeding grounds elsewhere and the number of birds in the area is at the seasonal low.

Mean weights were calculated from at least 30 weights for each species from birds trapped on Bolinas Lagoon or elsewhere in North America, from museum specimens, and from Johnston and McFarlane (1967), Easterla (1969), and Hamilton (1975). The mean number of birds of each species

TABLE 1
SEASONAL USE PATTERNS OF SHOREBIRDS ON BOLINAS LAGOON

1 Early arriving migrants	2 Early arriving, wintering	3 Late arriving, wintering	4 Breeding and wintering
Semipalmated Plover	Blacked-bellied Plover[a]	American Avocet	Killdeer
		Common Snipe	Snowy Plover
Ruddy Turnstone	Black Turnstone	Long-billed Dowitcher	
Whimbrel[a]	Marbled Godwit[a]	Dunlin	
Short-billed Dowitcher	Long-billed Curlew		
Red Knot	Greater Yellowlegs		
Western Sandpiper	Willet		
Baird's Sandpiper	Long-billed Dowitcher		
Pectoral Sandpiper	Sanderling		
Northern Phalarope	Least Sandpiper		

[a] Species for which evidence that adults migrate before juveniles in the fall comes from Bent (1927 or 1929).

on all censuses was calculated for each period. These means were multiplied by the mean weights to give the mean biomass of each species on Bolinas Lagoon in each period.

During fall periods we trapped small sandpipers (Page 1974a, b; Page et al. 1972) and made field observations of other species to determine when adults and juveniles first arrived and which species molted remiges at Bolinas Lagoon. We were able to separate the age classes of most species when they arrived in fall.

Between 1965 and 1976 personnel of Point Reyes Bird Observatory censused shorebirds at Limantour Estero, a small shallow estuary on Point Reyes, 21 km northwest of Bolinas Lagoon. Censuses at Limantour were less regular in relation to timing and tidal conditions than at Bolinas Lagoon. Limantour censuses included the major part but not the total amount of available shorebird habitat; a long arm of the estero near the mouth was omitted.

SEASONAL ABUNDANCE

Seasonal abundance patterns for regularly occurring shorebirds are illustrated for Bolinas Lagoon in Figures 2–4. From the abundance patterns and observations on the molt of birds four general strategies of shorebird use of the estuary were detected.

Strategy 1 used by nine species (Table 1) was to arrive early in fall and pass through Bolinas Lagoon before most of the adult and usually juvenile prebasic molt had been completed. Adult birds arrived prior to juveniles (Table 2). Wintering individuals occurred in small numbers or were absent but migrants of most species were relatively abundant in spring. A portion of the prealternate molt in some individuals of some species took place during spring migration at Bolinas Lagoon but this was not closely examined by us. The importance of Bolinas Lagoon to birds using this strategy was the support it provided to migratory staging birds; support during molt and during winter came largely from other areas.

Some variation within pattern 1 was exhibited by the Baird's Sandpiper (*Calidris bairdii*), the Pectoral Sandpiper (*Calidris melanotos*), and the Northern Phalarope (*Lobipes lobatus*) (Fig. 2). Adult Baird's and Pectoral sandpipers occurred rarely on fall migration so that juveniles made up almost all the birds observed

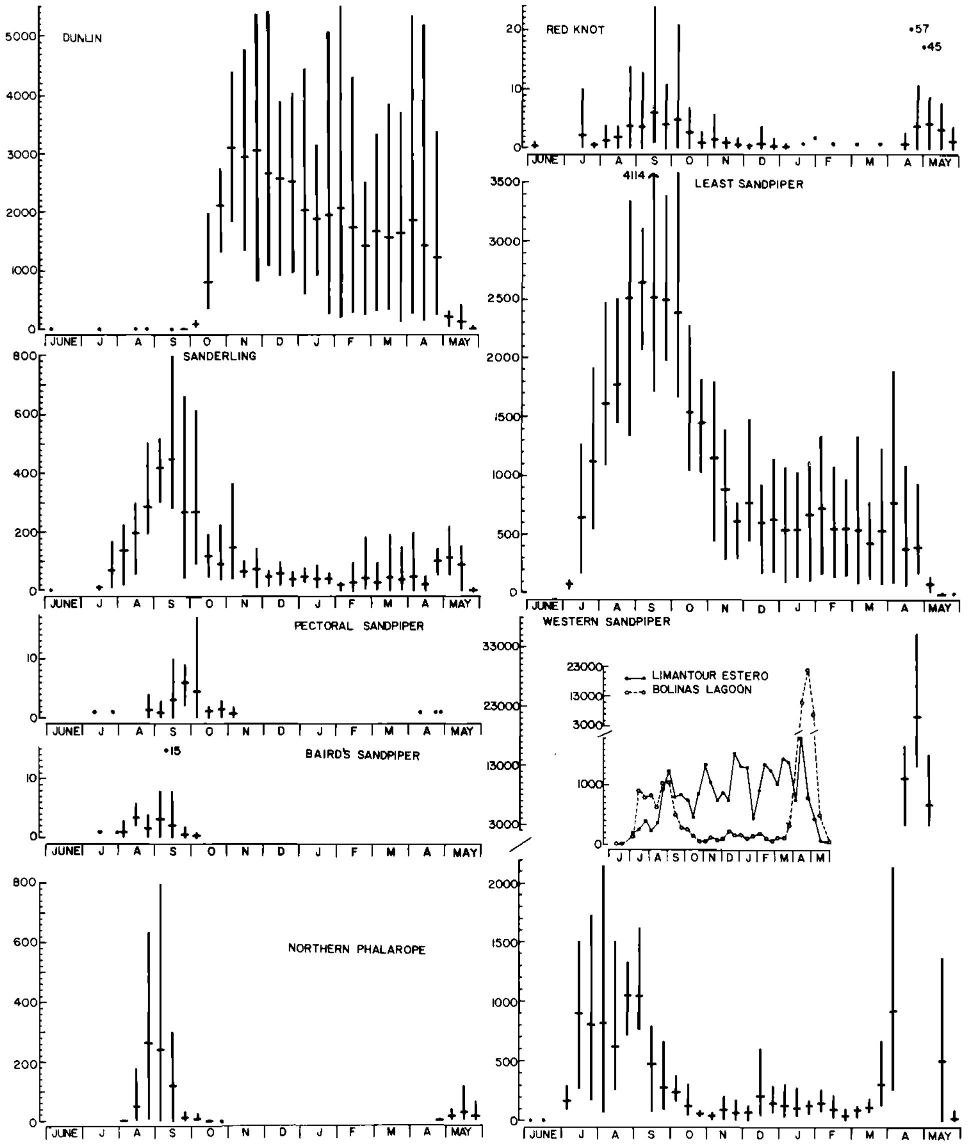

FIGURE 2. Seasonal abundance patterns of calidridine sandpipers and the Northern Phalarope on Bolinas Lagoon. Lines define extremes of high and low numbers observed in 10-day intervals over five years; horizontal lines indicate means. A dot indicates a single observation within a 5-day period, or an unusually high number of birds between census periods.

on Bolinas Lagoon; Baird's and Pectoral Sandpipers were very rare or absent in spring. The Northern Phalarope was the only species for which adult-before-juvenile migration in fall has not been reported in the North American literature or observed in our study, although such differential timing very likely occurs in California (D. W. Winkler pers. comm.). Juveniles greatly outnumbered adults in fall at Bolinas Lagoon and made up 93% of the 111 Northern Phalaropes banded there between 14 August and 19 September 1971. Most adults staged

TABLE 2
ARRIVAL DATES FOR ADULT AND JUVENILE SHOREBIRDS AT BOLINAS LAGOON

	Adult		Juvenile	
Species	First 1972	Usual	First 1972	First 1973
Semipalmated Plover	3 July	30 June–19 July	15 Aug	1 Aug
Ruddy Turnstone	17 July	5 July–19 July	17 Aug	15 Aug
Black Turnstone	5 July	30 June–9 July	20 Aug	no data
Greater Yellowlegs	17 July	5 July–9 July	18 Aug	12 Aug
Willet	no data	15 June–24 June	15 July	17 July
Short-billed Dowitcher	3 July	30 June–14 July	10 Aug	6 Aug
Red Knot	15 July	15 July–29 July	26 Aug	no data
Sanderling	17 July	10 July–19 July	31 Aug	21 Aug
Western Sandpiper	3 July	30 June–4 July	7 Aug	2 Aug
Least Sandpiper	3 July	30 June–4 July	10 Aug	30 July
Baird's Sandpiper	1 probable 15 July		9 Aug	30 July
Pectoral Sandpiper	1 on 13 July 1971, 21 and 25 July 1972		11 Sep	13 Sep

elsewhere making it difficult to detect temporal differences in migration between the two age groups. During spring migration Northern Phalaropes made sporadic appearances at Bolinas Lagoon, occurring in some years but not in others.

A second use pattern exhibited by nine species (Table 1), was characterized by the early fall arrival of migrating or wintering birds, adult-before-juvenile fall arrival, and a prebasic molt largely completed on Bolinas Lagoon. Some prealternate molt also took place on the estuary. Considerable variation occurred among these species in the size of the spring and fall migratory peaks. For most species of this group the estuary supported migratory staging individuals but, unlike the first group, it also supported numbers of molting and overwintering birds. Although relatively few Sanderlings (*Calidris alba*) occurred in winter compared to fall, this species is included with this group because many adults underwent much of their prebasic molt on the estuary. Many Sanderlings and Least Sandpipers (Page 1974b) probably left the area near or after completion of their prebasic molt (Fig. 2).

Short-billed Dowitcher (*Limnodromus griseus*) and Long-billed Dowitcher (*Limnodromus scolopaceus*) abundance patterns (Fig. 3) merit some discussion because of the difficulty of identifying the two species during censuses. Many observations between censuses using call notes and morphological characters to

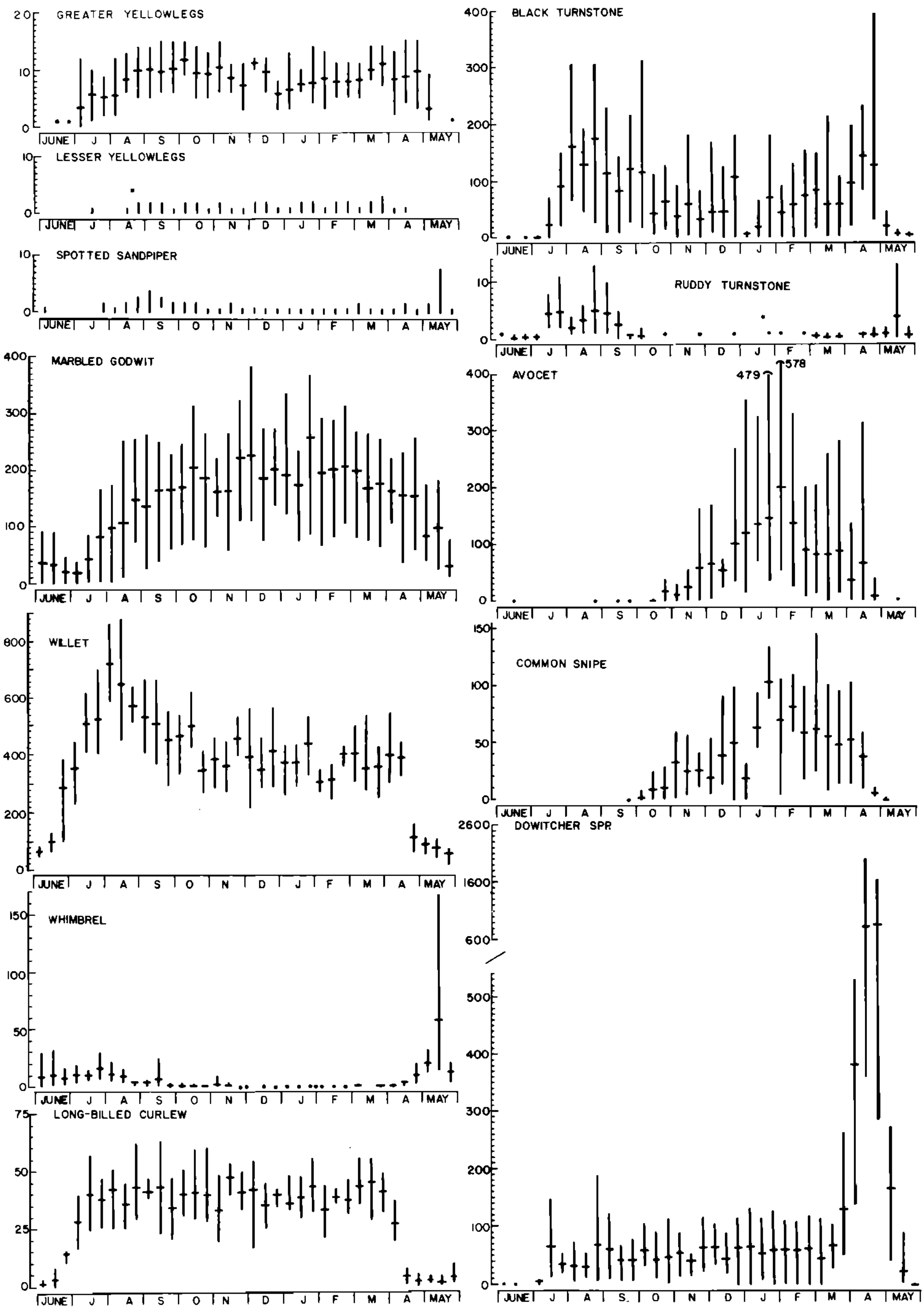

FIGURE 3. Seasonal abundance patterns of tringine sandpipers, curlews, turnstones, dowitchers, Common Snipe and Avocet. See Figure 2 for explanation.

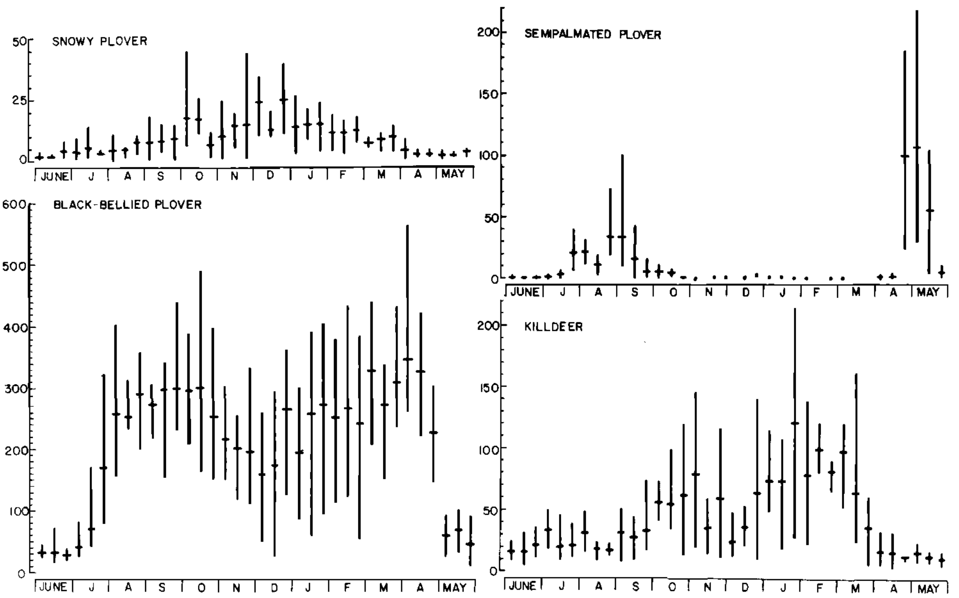

FIGURE 4. Seasonal abundance patterns of common plovers. See Figure 2 for explanation.

identify birds indicated that most dowitchers on Bolinas Lagoon from July through mid-September were short-bills and almost all birds between November and February were long-bills; the majority of dowitchers in April were short-bills. These plus other observations on molt confirmed that the Short-billed Dowitcher fits well into the first use pattern. During the 1975–76 season we found the first Long-billed Dowitchers on 31 July. These two individuals, and subsequent ones that appeared until the number had increased to nine birds, were adults that were all molting primaries on 26 August. The first immatures were identified in late September although they may have arrived earlier that month. That year about 75 Long-billed Dowitchers occurred during winter (November through February). Pitelka (1950) and Lenna (1969) reported that immature long-bills are more likely to be found than adults in coastal habitats, and Lenna (1969) observed that in the Point Reyes area, of which Bolinas Lagoon is a part, the species usually does not appear in fall until late September or early October. Probably in all years immatures form the bulk of long-bills wintering at Bolinas Lagoon; in some years the early arriving adults may not be present. More remains to be learned about Long-billed Dowitcher migration patterns at Bolinas Lagoon. We have tentatively placed it in two groups in Table 1 until further information becomes available.

Four species are listed under the third occurrence pattern (Table 1), including the Long-billed Dowitcher already discussed. The remaining three species arrive late in the fall (Figs. 2–3). Adult and juvenile Dunlins arrived simultaneously although at first juveniles heavily outnumbered adults in trapped samples (Page 1974a). Information on arrival times of adult and juvenile Common Snipes (*Capella gallinago*) and American Avocets (*Recurvirostra americana*) was not obtained in our study or in the literature. Adult prebasic molt was largely completed by the time the Dunlin (Holmes 1966, Page 1974a) and probably the other two

TABLE 3
RECORDS OF IRREGULARLY OCCURRING SHOREBIRDS AT BOLINAS LAGOON

Species	Numbers and dates
Himantopus mexicanus	1 on 21 Jan 1976
Pluvialis dominica	1 between 27 Aug 1974 and 11 Apr 1975 1 on 28 Aug and 2 Sep 1975[a] 1 adult on 9 occasions 8 Sep–17 Nov 1975[a] 2 on 9 Sep 1975[a] 1 on 12 and 22 Apr 1974
Limosa lapponica	1 between 26 Oct and 2 Dec 1973
Heteroscelus incanus	2 adults on 25 July 1973 1 adult on 29 July 1973 1 on 22 Aug 1974 1 on 30 Aug 1973
Aphriza virgata	1 on 7 Sep 1972 1 on 9 Oct 1971
Calidris acuminata	1 juvenile banded on 5 Oct 1972
Calidris ferruginea	1 juvenile 7–14 Sep 1974
Micropalama himantopus	1 adult on 7 and 13 July 1971
Steganopus tricolor	1 from 14 to 21 July 1972 (at least 2 different birds including an adult on 17 and 21 July) 7 on 26 July 1973 4 on 1 Aug, 1 on 4 Aug 1975 3 on 7 Aug 1972, 2 adults and 1 unknown age
Phalaropus fulicarius	1 on 23 Oct and 15 Nov 1972 3–75 from 2 Nov to 1 Dec 1973 1 on 16 Nov 1971 3 on 17 Apr and 3–44 from 11 to 21 May 1976 2 on 11 May 1974 1 on 2 June 1971

[a] These were singletons or at most two individuals.

species (Palmer 1967, Gibson 1971, Tuck 1972) arrived at Bolinas Lagoon. Fall and to a much lesser extent spring passages of migrants were apparent in the Dunlin but not in the snipe or the avocet.

The Killdeer (*Charadrius vociferus*) and Snowy Plover (*Charadrius alexandrinus*) make up a fourth group which includes only species that breed on Bolinas Lagoon (Fig. 4). Resident numbers were augmented and perhaps even replaced beginning in late August for the Snowy Plover and in September for the Killdeer; the duration of immigration into the area was not clearly defined because of difficulties in censusing these species. Some adults underwent prebasic molt and undoubtedly also prealternate molt in the area. Convincing evidence of fall or spring migratory passages was not found for either species. Fluctuations of Killdeer numbers in November and December were most likely related to local movements of birds between pastures and the estuary rather than to true migratory movements.

A fifth group consists of uncommon or irregularly occurring species. These include the regularly occurring but uncommon Spotted Sandpiper (*Actitis macularia*), and the Lesser Yellowlegs (*Tringa flavipes*). Their seasonal abundance patterns are illustrated in Figure 3. An additional ten irregularly occurring species are listed with dates of occurrence in Table 3.

Seasonal occurrence patterns sometimes varied somewhat among species within the groups listed in Table 1. Thus Willet (*Catoptrophorus semipalmatus*) and Least Sandpiper patterns while conforming to the generalities previously described for birds in the second group differed in that non-breeding Willets regularly oversummered at Bolinas Lagoon whereas Least Sandpipers did not (Figs. 2–3). In fact, large non-breeding shorebirds such as the Willet, Marbled Godwit (*Limosa fedoa*), Black-bellied Plover (*Pluvialis squatarola*), and Whimbrel (*Numenius phaeopus*) occurred regularly on Bolinas Lagoon in June unlike members of most smaller species (Figs. 3–4).

Abundance patterns sometimes probably reflected local rather than widespread population shifts. This has already been mentioned for the Killdeer and is probably reflected in the Black-bellied Plover by the dip in November and December, and in the Black Turnstone (*Arenaria melanoleuca*) by the dip in January (Figs. 3–4). Both of these species used areas away from the estuary, and in winter, departure near or at high tide sometimes occurred prior to the completion of a census, resulting in undercounts of these species. These winter undercounts occurred mostly when high winds and rainfall increased the rate at which the tide flooded the tidal flats.

The seasonal abundance graphs formulated for Bolinas Lagoon (Figs. 2–4) do not necessarily represent species abundance patterns in other California estuaries. This was particularly apparent when Western Sandpiper numbers at Bolinas Lagoon and Limantour Estero were compared (Fig. 2). At Bolinas Lagoon the abundance pattern was characterized by a large fall and a massive spring migratory peak but a relatively low winter population. At Limantour Estero winter numbers were generally similar to fall numbers and there was only a slight indication of a spring migratory peak, mostly as a result of unusually high spring numbers in 1976. Bolinas Lagoon was important to Western Sandpipers as a fall and spring migratory staging area; Limantour Estero was important as an overwintering area. At Bay Farm Island, Storer (1951) found yet another abundance pattern for the Western Sandpiper. Other variability in abundance patterns at different California estuaries can be expected as more areas are examined.

SPECIES COMPOSITION BY NUMBERS AND BIOMASS

The percent composition of species by number and biomass during three periods are given for Bolinas Lagoon's shorebird fauna in Table 4. Individuals of small species, with mean weights of less than 150 g (Table 4), collectively outnumbered larger species, with mean weights exceeding 150 g, by ratios of 3:1 in fall and winter and 9:1 in spring. But larger species dominated in biomass. Larger species made up 75, 65 and 48% of the total biomass in fall, winter and spring respectively. The morphologically similar Least Sandpiper, Western Sandpiper and Dunlin varied considerably in relative abundance during the three periods; Least Sandpipers were most numerous in fall, Dunlins in winter and Western Sandpipers in spring. These relative abundance changes support Recher's (1966) hypothesis that small morphologically similar shorebirds may reduce competition by staggering their peak periods of abundance in a particular area. Since a similar staggering of abundance does not appear to occur, at least between the

TABLE 4

THE SHOREBIRD FAUNA OF BOLINAS LAGOON; PER CENT COMPOSITION BY NUMBER (N) AND BIOMASS (B)[a]

Species	Per cent composition						Mean weight (g)
	Fall		Winter		Spring		
	N	B	N	B	N	B	
Least Sandpiper	44.2	9.4	15.8	3.1	4.8	1.6	20.5
Western Sandpiper	14.1	3.6	2.5	0.6	63.5	26.4	25.0
Northern Phalarope	1.4	0.4	0	0	0.1	*	30.1
Snowy Plover	0.2	0.1	0.3	0.1	0.1	*	40.3
Semipalmated Plover	0.3	0.2	*	*	0.4	0.3	45.6
Dunlin	6.4	3.3	53.3	25.6	15.1	12.6	50.1
Sanderling	4.8	2.9	1.2	0.7	0.8	0.7	58.0
Killdeer	0.9	0.8	1.6	1.3	0.4	0.7	89.2
Ruddy Turnstone	0.1	0.1	*	*	*	*	101.7
Common Snipe	0.1	0.1	1.1	1.1	0.4	0.7	104.0
dowitcher spp.	1.1	1.4	1.3	1.4	3.9	7.5	113.6
Black Turnstone	2.4	2.9	1.1	1.3	0.9	1.8	116.8
Red Knot	0.1	0.1	*	*	*	0.1	150.9
Greater Yellowlegs	0.2	0.4	0.2	0.3	0.1	0.3	182.4
Black-bellied Plover	6.0	13.6	5.2	10.9	3.1	11.3	219.1
Willet	13.1	40.5	8.6	24.8	3.4	17.1	299.3
American Avocet	*	0.1	2.2	6.5	0.6	2.9	312.0
Marbled Godwit	3.2	12.4	4.5	16.2	1.9	11.8	371.4
Whimbrel	0.2	0.6	*	*	0.2	1.1	378.9
Long-billed Curlew	1.0	7.1	0.9	5.9	0.3	3.0	691.3

[a] Percentages by number and biomass were calculated from mean census numbers over the five-year study period. An asterisk indicates a percentage >0 and <0.05%. Species not included contributed less than 0.05% of numbers and biomass during all periods.

Western Sandpiper and Dunlin during winter at Limantour Estero, other behavioral differences must also serve to reduce competition between these species.

ANNUAL VARIATIONS IN NUMBERS

Some species such as the Northern Phalarope varied considerably while others such as the Willet remained remarkably constant in number from season to season at Bolinas Lagoon (Table 5). American Avocets and Marbled Godwits increased in numbers over the five-season study period; mean winter numbers of godwits rose from 96 to 298 and avocet winter numbers from 37 to 252 over the study period. In contrast mean fall numbers of Northern Phalaropes declined from 161 to 1 over the five seasons. Whether this decline of Northern Phalaropes represented a significant change in the species' occurrence on the estuary or was just an artifact of a generally erratic migration pattern was not clear. The high magnitude of variation for Sanderlings in the spring period (Table 5) resulted from the unexplained absence of Sanderlings from the estuary in March and early April of some years but not others.

Variability in Dunlin and Least Sandpiper mean winter and spring numbers (Table 5) was correlated with rainfall (Table 6). Heavy rainfall caused flooding of the estuary and resulted in decreased tidal flat availability. The winters of heaviest rainfall corresponded with the lowest winter numbers of Dunlins and Least Sandpipers (Table 6). Rain probably created fresh water habitats and may affect the

TABLE 5
ANNUAL VARIATION IN SHOREBIRD NUMBERS AT BOLINAS LAGOON, 1971–72 THROUGH 1975–76 SEASONS

	Range in mean number			Mean over 5 years			Magnitude of variation[b]		
Species	F[a]	W	S	F	W	S	F	W	S
American Avocet		35–252	7–137	2	95	40		7.2	19.6
Black-bellied Plover	182–268	110–304	174–271	236	228	223	1.5	2.8	1.6
Semipalmated Plover	8–17		15–53	13		30	2.1		3.5
Killdeer	25–43	48–93	14–50	34	69	32	1.7	1.9	3.6
Snowy Plover	6–13	8–19	3–7	9	15	5	2.2	2.4	2.3
Marbled Godwit	38–189	96–298	60–181	127	199	137	5.0	3.1	3.0
Whimbrel	3–9		5–24	6		12	3.0		4.8
Long-billed Curlew	28–46	35–44	15–21	39	39	19	1.6	1.3	1.4
Greater Yellowlegs	7–10	6–11	6–8	8	8	7	1.4	1.8	1.3
Willet	445–575	335–425	219–288	515	379	246	1.3	1.3	1.3
Black Turnstone	33–159	17–86	32–117	94	49	65	4.8	5.1	3.7
Northern Phalarope	1–161		0.1–23	56		6	201.3		230.0
Common Snipe		44–61	18–52	2	50	30		1.4	2.9
dowitchers	24–73	20–94	124–447	45	59	284	3.0	4.7	3.6
Sanderling	147–285	41–88	17–123	189	54	54	1.9	2.1	7.2
Western Sandpiper	391–747	67–138	2264–5834	552	108	4565	1.9	2.1	2.6
Least Sandpiper	1430–2154	295–1071	109–824	1736	693	343	1.5	3.6	7.6
Dunlin	236–282	1040–4304	284–2790	253	2341	1089	1.2	4.1	9.8
Total shorebirds	3664–4482	2746–7076	4091–10,887	3923	4380	7184	1.2	2.6	2.7

[a] F, fall; W, winter; S, spring.

[b] Magnitude of variation is the highest divided by the lowest yearly mean.

salt water–fresh water distribution of these two small shorebirds. Since substantial variation in shorebird numbers on an estuary may occur from year to year, one season's censuses do not completely measure the capacity of an area to hold shorebirds; only several years of censuses will do that.

USE OF INTRAESTUARINE HABITATS

Shorebirds used the salt marsh on Bolinas Lagoon as a feeding and roosting area. Willets, Least Sandpipers and Pectoral Sandpipers often fed in the salt marsh; Black-bellied Plovers, Long-billed Curlews (*Numenius americanus*) and Common Snipes occasionally fed there. The salt marsh was most important to shorebirds as a high-tide and night-time roost. At high tides most species roosted

TABLE 6
RAINFALL AND WINTER NUMBERS OF SANDPIPERS AT BOLINAS LAGOON

Season	1971–72	1972–73	1973–74	1974–75	1975–76
Inches of rain[a]					
1 Oct–28 Feb	19.0	50.2	34.5	22.1	13.6
Mean winter number[b]:					
Dunlin	2268	1187	1040	2906	4304
Least Sandpiper	773	295	344	981	1071
Total shorebirds	4093	2786	2746	5197	7076

[a] Rainfall was recorded at a station about 6 km from Bolinas Lagoon.

[b] Numbers of birds are means from November through February censuses.

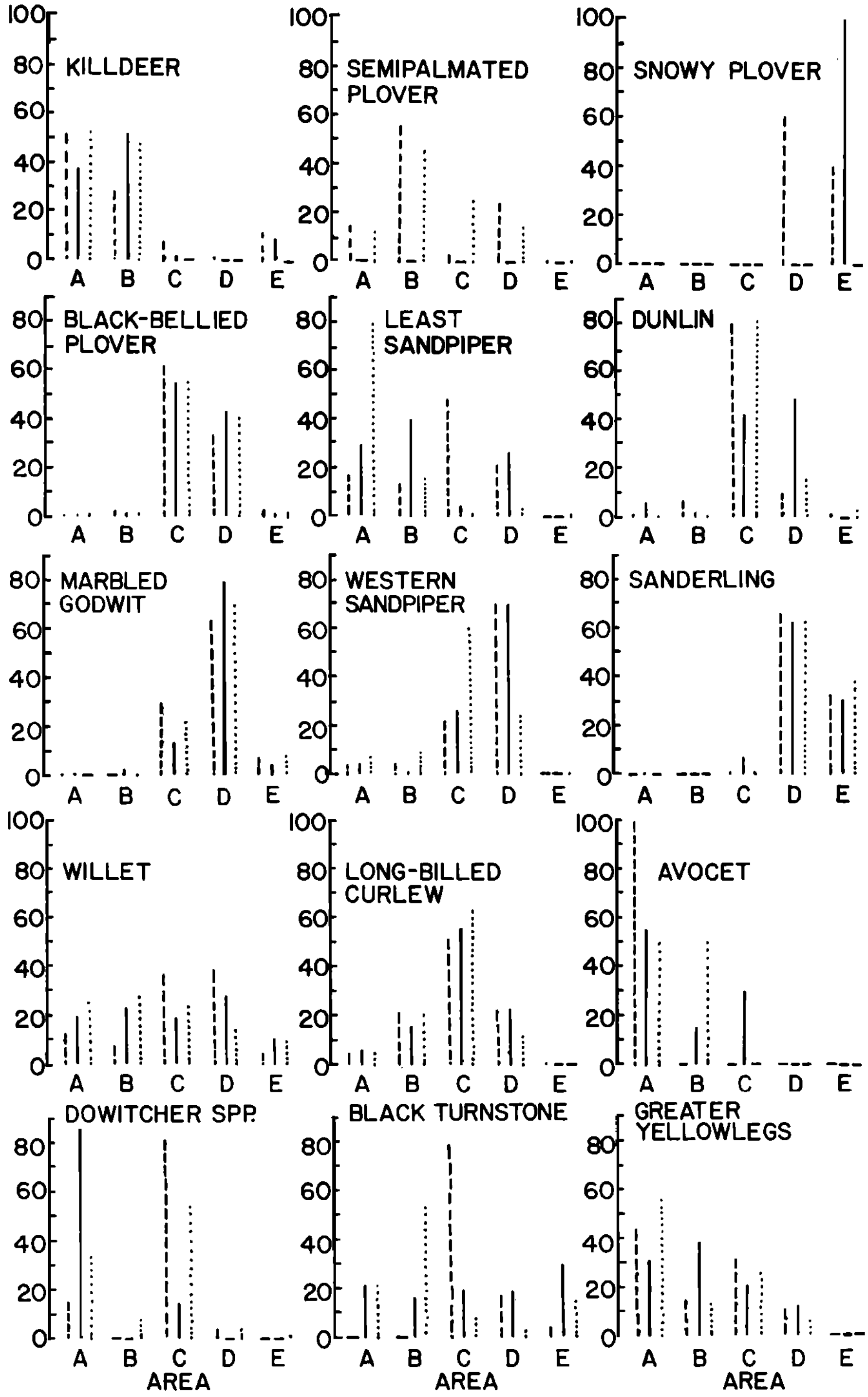

FIGURE 5. Per cent occurrence of shorebirds on five areas of tidal flats on Bolinas Lagoon during fall (dashed line), winter (solid line) and spring (dotted line). Data are corrected to eliminate bias resulting from differences in area sizes.

TABLE 7
VARIATION IN SHOREBIRDS USE OF DIFFERENT TIDAL FLAT AREAS ON BOLINAS LAGOON

	Mean number of species per census			Mean number of birds/10 ha per census			Mean biomass of birds per census (kg/10 ha)			Mean area exposed per census		
Area	F[a]	W	S	F	W	S	F	W	S	F	W	S
A	5.0	5.8	4.7	99	94	294	7.2	9.3	12.3	51	50	50
B	4.2	4.7	3.6	90	93	287	5.5	9.5	12.5	50	51	48
C	7.6	6.1	6.2	387	171	717	36.6	23.5	33.6	69	68	71
D	7.2	5.8	5.6	382	271	328	36.4	37.9	27.6	61	62	58
E	3.2	2.6	2.5	41	21	45	5.5	4.5	4.4	39	43	37

[a] F, fall; W, winter; S, spring.

in the high-tide zone of the tidal flat. If high tides forced the birds from these areas they usually moved into the salt marsh or the sand beach on Kent Island. Most Long-billed Curlews, Willets, Marbled Godwits and some Least Sandpipers usually moved into the salt marsh; many other species moved to the sand beach. Least Sandpipers, Dunlins, Western Sandpipers and dowitchers regularly used the salt marsh as a nighttime roost.

The tidal flat was by far the most important feeding habitat. On the tidal flat shorebirds segregated into areas with different types of substrate (Fig. 5). The Killdeer, Greater Yellowlegs (*Tringa melanoleuca*), American Avocet and Least Sandpiper fed on the muddiest substrates and were prominent shorebirds in areas A and B. The Snowy Plover and Sanderling occurred most frequently in areas D and E where the sediment was coarser. The Black-bellied Plover, Dunlin, Western Sandpiper and Marbled Godwit were most abundant in areas C and D (Fig. 5). Lenna (1969) reports that the two species of dowitchers feed in different habitats in the Point Reyes area. According to him, the Short-billed Dowitcher occurs primarily during fall and prefers sandier tidal flats than the Long-billed Dowitcher which occurs primarily during winter. During spring both species occur simultaneously at Bolinas Lagoon. Our census data generally agree with Lenna's (1969) observations; dowitchers were most abundant in area C in fall, in area A in winter and in areas A and C in spring (Fig. 5).

The distribution of some shorebirds could not easily be related to substrate differences. The Willet was more scattered over the different areas than any other shorebird (Fig. 5). The distribution of Long-billed Curlews was probably related to the distribution of its major prey rather than to substrate type (Stenzel et al. 1976). The Black Turnstone's distribution was undoubtedly influenced by the location of algae on the tidal flat, but we did not measure algal abundance in the five areas and were not able accurately to demonstrate this point.

Among the five tidal flat areas the number and biomass of birds censused per unit area varied substantially (Table 7). In area E, the sandiest area, shorebird density and biomass were lowest; in areas C and D, tidal flats of intermediate substrate texture, density and biomass were highest. A similar trend was also apparent for the mean number of species observed per census (Table 7). Therefore, not only did areas C and D support more birds and a greater biomass but they also supported a wider variety of species than the other areas.

TABLE 8

PER CENT OF SHOREBIRDS USING OUTER COAST HABITATS[a]

Species	Per Cent				
	Fall		Winter		Spring
Black-bellied Plover	4.5		8.0		4.4
Black Turnstone	13.4	*	43.0		39.8
Willet	9.2	*	16.4		14.4
Marbled Godwit	2.6	*	7.4		7.3
Sanderling	5.6	*	51.0	*	11.7

[a] Based on census data from Bolinas Lagoon and 8.5 km of adjacent open coast taken from July 1973 through May 1974. An asterisk indicates a significant difference ($P < 0.05$) between adjacent percentages.

USE OF EXTRALIMITAL HABITAT

The 8.5 km of open coast adjacent to and north of Bolinas Lagoon was used by several species that also occurred on the estuary. Birds were often seen flying between the estuary and coast indicating that both areas were used by some individuals. Except for summer on the open coast we consistently found Willets, Black Turnstones, Sanderlings, Least Sandpipers, Black-bellied Plovers, Marbled Godwits, Killdeers, and a Spotted Sandpiper; in addition during migration periods we regularly found Whimbrels. Semipalmated Plovers (*Charadrius semipalmatus*), Ruddy Turnstones (*Arenaria interpres*), Baird's Sandpipers, Dunlins, dowitchers, Red Phalaropes (*Phalaropus fulicarius*), and Northern Phalaropes occurred sporadically along the coast. A greater proportion of the estuary-open coast population of some species occurred along the coast in the winter than in the fall period. Black Turnstones and Sanderlings substantially increased their relative use of the open coast from fall to winter and smaller but significant increases were noted for the Willet and Marbled Godwit (Table 8). The relative increase in the use of the coast from fall to winter may have been due to increased pressure on birds to use more of the available feeding habitat in the Bolinas area in winter (Stenzel et al. 1976).

After the winter rains began in October or November each year, some shorebirds used the pastures on Bolinas mesa. Most of the Black-bellied Plovers and Dunlins and some Least Sandpipers from the estuary moved there and fed or roosted during high tides and rain. During the winter a few Killdeers and snipes feed in the pastures regardless of the tides. Greater Yellowlegs, Western Sandpipers, and dowitchers also used the mesa pastures occasionally. On the Ythan Estuary in Scotland, Goss-Custard (1969) found that pastures can be important alternate feeding habitat for Redshanks (*Tringa totanus*) during winter. These observations suggest that habitats outside the commonly observed boundaries of an estuary may directly contribute to the support of the birds using the estuary.

INTERESTUARINE VARIATIONS IN SHOREBIRD DENSITIES

Shorebird densities varied markedly between Bolinas Lagoon and Limantour Estero (Table 9), two relatively similar estuaries located 21 km apart. Greater densities of Killdeers and Common Snipes at Bolinas Lagoon were undoubtedly related to the greater amount of marshy pastureland bordering Bolinas Lagoon

TABLE 9

Seasonal Variation in Mean Densities (no./100 ha) of Shorebirds in Bolinas Lagoon (B) and Limantour Estero (L)[a]

	Fall		Winter		Spring		Magnitude of variation[b]		
Species	B	L	B	L	B	L	Fall	Winter	Spring
American Avocet	0.3	0.1	21.3	0.1	9.0	0	3.0	213.0	?
Black-bellied Plover	52.8	13.3	51.0	18.4	49.9	3.8	4.0	2.8	13.1
Semipalmated Plover	2.9	7.7	0.1	4.8	6.7	7.1	2.7	48.0	1.1
Killdeer	7.6	2.2	15.4	1.8	7.2	1.3	3.5	8.6	5.5
Snowy Plover	1.9	6.2	3.4	19.2	1.1	6.6	3.3	5.6	6.0
Marbled Godwit	28.4	12.4	44.5	19.6	30.7	3.6	2.3	2.3	8.5
Whimbrel	1.4	1.3	0.1	0.1	2.7	1.1	1.1	1.0	2.5
Long-billed Curlew	8.7	0.3	8.7	0.3	4.3	0.2	29.0	29.0	21.5
Greater Yellowlegs	1.8	0.4	1.8	0.6	1.5	0.9	4.5	3.0	1.7
Willet	115.2	61.6	84.8	73.9	55.0	33.7	1.9	1.1	1.6
Black Turnstone	21.0	10.0	11.0	6.5	14.5	6.2	2.1	1.7	2.3
Northern Phalarope	12.5	2.7	0	0.1	1.4	<0.05	4.6	?	?
Common Snipe	0.5	0.1	11.2	0.2	6.7	0	5.0	56.0	?
dowitchers	10.1	9.2	13.2	1.5	63.5	5.8	1.1	8.8	10.9
Sanderling	42.3	85.9	12.1	70.5	12.1	51.4	2.0	5.8	4.2
Western Sandpiper	123.5	313.7	24.2	548.5	1021.5	432.1	2.5	22.7	2.4
Least Sandpiper	388.5	99.4	155.1	100.5	76.8	47.5	3.9	1.5	1.6
Dunlin	56.6	101.6	523.8	843.4	243.7	222.0	1.8	1.6	1.1

[a] Data derived from five seasons of censusing at Bolinas Lagoon and ten seasons at Limantour Estero.

[b] Magnitude of Variation is the higher mean density divided by the lower for each period. Species whose densities did not reach 1.0 birds/100 ha in any period were excluded. Queries (?) indicate unreasonable quotients because of zero or minor fractional values for either location.

compared to Limantour Estero, whereas greater densities of Snowy Plovers and Sanderlings at Limantour Estero were likely related to the greater extent of sandy habitat at Limantour Estero compared to Bolinas Lagoon. Marked differences in avocet densities between the two estuaries may also have been due to differences in habitat type since Bolinas Lagoon has larger low intertidal areas of muddy substrate than Limantour Estero. Other observed differences in shorebird densities such as occurred for the Semipalmated Plover in winter, Black-bellied Plover in spring, Long-billed Curlew at all periods and Western Sandpiper as previously mentioned are difficult to account for on the basis of obvious habitat differences between the two estuaries. Only careful study will clarify these differences.

DISCUSSION

Our shorebird censusing studies provide insights into avian numerical variation in wetland habitats that should be considered for the interpretation of water bird census data. Obviously censuses from only part of a season (bird year) give a distorted view of a wetland's use by birds. Censuses conducted regularly over an entire season reveal the abundance patterns for most species for that area but not necessarily the total number of birds the area can support; this varies from year to year. Censuses from part of a wetland form an unreliable index of what is present in the whole; only thorough knowledge of the habitat distribution within the whole system would make extrapolation from the part to the whole possible and to date a comprehensive description of wetland habitat as it relates to birds has not been developed. Censuses from discrete wetlands can not even be relied upon to provide general species abundance patterns for other wetlands as was illustrated by the discrepancies observed in the Western Sandpiper abundance patterns between Limantour Estero and Bolinas Lagoon.

The many factors that determine the number and kinds of birds that are found in a wetland are difficult to separate. Certainly the wetland must provide an acceptable physical environment and food resource for the birds. The surrounding environment plays an important role when it contributes to the overall needs of birds using the wetland. Annual variations in productivity on the breeding grounds may also be reflected in the overall numbers and the adult to juvenile ratios of shorebirds in a wetland. Tradition may partially determine where birds occur locally; it has often been demonstrated that individual shorebirds return to the same wetland to overwinter year after year (Page 1974a, Kelly 1976, P. G. Connors pers. comm.). The presence of Long-billed Curlews and American Avocets at Bolinas Lagoon and their absence in other wetlands in the Point Reyes area in winter may be related more to traditional patterns than other differences between the areas.

Our observations reveal that an estuarine habitat–complex, rather than being uniform in the densities of birds supported, is really quite variable. These observations imply that destruction of part of a wetland may result in habitat loss for some species that is not easily substituted for by remaining habitat nearby. Even species with a high tolerance for a broad range of different habitats may, in the event of being displaced from traditional wintering areas, find alternative sites filled to capacity. Even if a group of adjacent wetlands does not support the full complement of birds it is capable of holding, reduction of the wetland's area may still have detrimental long-term effects for birds because the flexibility for choice between areas is reduced; this could have important consequences during years of some restriction such as drought.

Over relatively small geographical distances there must definitely be an additive effect within a wetland system such that the whole system is able to support more than the sum of its parts if each part were totally independent. The basis for this concept can be observed on Point Reyes when small shorebirds from Drake's Estero fly 2.5 km to Abbott's Lagoon at high tide in winter to roost and feed and then return to Drake's Estero at a lower tide. These birds would not likely appear at Abbott's Lagoon if Drake's Estero were not nearby. Whether as many small shorebirds would overwinter at Drake's Estero if Abbott's Lagoon did not exist can not definitely be stated although it is evident that Abbott's Lagoon contributes positively to the support of small sandpipers wintering in Drake's Estero. Obviously considerable study remains before a thorough appreciation of the factors promoting the uneven spatial and temporal distribution of water birds in California's coastal wetlands will emerge.

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HABITAT UTILIZATION BY WINTERING AND MIGRATING SHOREBIRDS ON HUMBOLDT BAY, CALIFORNIA

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ABSTRACT.—During 1968–69, a study was made of shorebirds on Humboldt Bay, California. Eight different shorebird habitat types were recognized, and 34 different species of shorebirds used them. Five additional species were recorded as vagrants only.

The mud flat habitat was found to be the most important with 29 species occurring. Three (Willet, Marbled Godwit and Black-bellied Plover) were recorded there in more than 75 percent of censuses. Average density throughout the year was 33 birds per hectare. Seasonally, the highest number of species occurred in the fall, the highest density in the spring.

As the incoming tide flooded the mud flats, most birds roosted on the salt marsh surrounding the bay; however, extremely high tides would force all birds to uplands or freshwater marshes. At high tide some species such as the Black-bellied Plover, Killdeer and Least Sandpiper moved directly to upland areas. Heavy use of uplands did not occur until after the first rains in late fall. Such use increased further after heavy rains washed silt and debris onto mud flats. A sewage pond was used by 21 species, the most frequent being the Least Sandpiper and the most dense the Northern Phalarope.

Movement during winter centered about availability of mud flats as feeding area. Few birds were found using other areas when mud flats were available. When tides limited daytime use of mud flats, alternate feeding areas became important. But salt marsh was used as feeding area by only eight species, just prior to or after high tide. An exodus from the area was noted when alternate areas became unavailable because of flooding. Little movement occurred between extreme ends of the bay except during migration. Few locally marked birds were seen at other California stations.

Recent investigators on the Pacific Coast have recognized 11 habitat types used by shorebirds. Storer (1951) found five in his small study area on San Francisco Bay and later Recher (1966) studied 10 in a much broader study. Smail and Lenna (1969) identified eight habitats in a coastal estuary north of San Francisco Bay. All recognized the importance of the mud flat habitat but also the diversity needed by shorebirds in intertidal areas.

Humboldt Bay on the north coast of California is known to be a major migration and wintering area for shorebirds. Little has been documented concerning their numbers, species composition, seasonal movement and use of available habitats. This paper deals with the habitat utilization by wintering and migrating shorebirds of this bay. The study was conducted in 1968 and 1969 (Gerstenberg 1972).

STUDY AREA AND METHODS

Humboldt Bay is a long narrow coastal bay about 24 kilometers long. It is protected from the ocean by two narrow sand spits and is roughly hour-glass in shape with an outlet to the sea in the middle. There are four small freshwater creeks which empty into the east side of the bay.

Nine shorebird habitats were present in Humboldt Bay (Table 1) and systematic censusing was done in eight. An intertidal zone occurred at both jetties of the harbor entrance which was not censused.

There were 2950 hectares of mud flat available at mean low tide. Because time and height of low tide varies from day to day, the amount of mud flat available to feeding birds varies daily and seasonally.

In mid channel near the mouth of Elk River and on the south spit of the bay the substrate is coarse forming sand flats. There were sand islands in North Bay that were formed when the channels were deepened. Sand beaches occurred on the seaward side of both spits.

Along the shore and extending through the mud flats into the fields and freshwater creeks were

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TABLE 1
SHOREBIRD USE OF EIGHT HABITAT TYPES AT HUMBOLDT BAY, CALIFORNIA, 1968–1969[a]

Species	Mud flat	Sand flat	Tidal slough	Salt marsh	Up-land	F/W marsh	Sewage pond	Sand beach
PLOVERS								
Black-bellied Plover	77.7	81.4	46.3	40.7	78.4	6.4		28.6
	3.93	9.32	5.89	16.18	6.02	0.05		15.32
Killdeer	9.0	21.0	44.2	7.4	78.4	59.6	22.8	28.6
	0.16	0.46	3.63	0.07	1.36	0.73	0.20	0.30
Black Turnstone	27.9	60.5	68.8	29.6			0.9	
	0.64	2.29	36.57	0.57			0.01	
Ruddy Turnstone	12.5	18.5	4.6	11.1	9.8		3.5	
	0.23	0.28	0.30	0.15	0.01		0.01	
Semipalmated Plover	12.9	35.8	7.0	7.4		9.0	3.5	14.3
	0.28	2.03	2.03	0.77		0.18	0.01	0.15
Snowy Plover		1.3						42.8
		0.01						1.32
Golden Plover		1.3		3.6	8.3			14.3
		0.01		0.02	0.01			0.15
SHORT-LEGGED SHOREBIRDS								
Dunlin	45.3	43.2	44.2	48.2	51.0	6.4	21.9	
	54.80	24.46	35.58	124.80	35.83	0.53	0.25	
Western Sandpiper	56.8	59.2	27.9	40.7	58.8	12.8	47.4	28.6
	48.19	24.83	49.05	596.80	10.37	2.12	1.94	3.68
Least Sandpiper	46.3	38.3	53.5	7.4	52.9	28.4	70.2	28.6
	11.34	3.29	25.20	0.82	0.56	2.52	4.42	56.83
Sanderling	27.5	80.2						100.0
	6.30	32.37						68.94
Northern Phalarope	1.0				7.8	2.8	51.7	
	0.07				0.02	0.02	22.49	
Red Phalarope	0.3				2.1	3.2	22.6	28.6
	0.01				0.01	0.31	1.32	0.74
Wandering Tattler	4.1	11.2						
	0.01	0.12						
Wilson's Phalarope	0.7						12.2	
	0.01						0.15	
Spotted Sandpiper	0.3	1.3				1.1	13.8	
	0.01	0.01				0.01	0.06	
Pectoral Sandpiper	0.3			3.6	2.1		2.6	
	0.01			0.02	0.01		0.01	
Rock Sandpiper	0.3							
	0.01							
Sharp-tailed Sandpiper					2.1			
					0.01			
Rufous-necked Sandpiper	0.3							
	0.01							
Semipalmated Sandpiper							0.9	
							0.01	

TABLE 1. (CONTINUED)

Species	Mud flat	Sand flat	Tidal slough	Salt marsh	Up-land	F/W marsh	Sewage pond	Sand beach
MEDIUM SIZED SHOREBIRDS								
Dowitcher	46.3	30.8	44.2	59.3	41.6	31.2	35.2	14.3
(two species)	18.16	17.42	17.30	128.50	1.63	0.74	0.46	0.15
Greater Yellowlegs	10.1	2.5	20.9	7.4	60.8	46.8	1.7	
	0.10	0.02	1.36	0.07	0.10	0.53	0.01	
Knot	4.2	9.9		7.2	6.0			
	0.12	1.11		0.57	0.01			
Common Snipe				3.6	18.7	58.8	3.5	
				0.02	0.04	3.46	0.02	
Lesser Yellowlegs	0.7		4.4		8.3		6.1	
	0.01		0.15		0.01		0.02	
Stilt Sandpiper	0.3	1.3		3.6				
	0.01	0.01		0.02				
LONG-LEGGED SHOREBIRDS								
Marbled Godwit	86.4	76.5	53.5	74.1	7.8	1.0	1.8	14.3
	18.29	5.15	6.81	338.50	0.43	0.01	0.66	0.15
Willet	85.7	76.5	93.0	66.7	3.9	11.8	12.3	57.1
	6.89	4.04	54.86	63.26	0.10	0.47	0.11	0.59
Long-billed Curlew	26.8			37.0	2.0			
	0.26			2.40	0.02			
Whimbrel	10.8	13.6	16.3	7.2				28.6
	0.09	0.19	0.99	7.97				0.30
American Avocet	8.7			18.5	2.0		7.9	
	0.19			0.17	0.01		0.47	
Bar-tailed Godwit	0.7							
	0.01							
Number of visits	294	84	45	23	49	119	115	8
Hectares censused	48.08	14.16	1.54	15.58	93.08	10.44	20.23	4.86
Ave. no./census/5 ha	33.32	25.50	48.76	329.40	10.95	2.11	6.60	26.72

[a] For each species, the upper row of values are frequencies, or percent of censuses in which each was recorded; the lower row gives the average number of individuals per 5 ha per census.

large tidal sloughs. Old pilings and small mud flats were found along the banks, some of which had log rafts attached.

Adjacent to the mud flats and elevated 5 to 100 cm were salt marshes. Much of this habitat had been removed when a dike was built in the early 1900's around most of the bay. The marshes were dominated either by a mixture of common pickleweed (*Salicornia pacifica*) and salt grass (*Distichlis spicata*) or by cord grass (*Spartina foliosa*). The diked area on the landward side consisted mainly of seeded pastures (red clover *Trifolium pratense*, velvet grass *Holcus lanatus*, bent grass *Agrostis* sp., Italian rye grass *Lolium multiflorum* and orchard grass *Dactylis glomerata*) with meandering channels which drained water. Livestock grazed the pastures closely and were periodically removed to allow the vegetation to regrow. During the rainy season the pastures became saturated with water and scattered ponds were formed in the lower areas. Permanent freshwater marshes were created in low areas of poor drainage.

In 1957 the City of Arcata built a 20-ha oxidation pond for secondary sewage treatment on the north side of the bay. This large freshwater pond provided water, food and roosting sites for many species of birds. Water parsley (*Oenanthe sarmentosa*) and knotweed (*Polygonum persicaria*) oc-

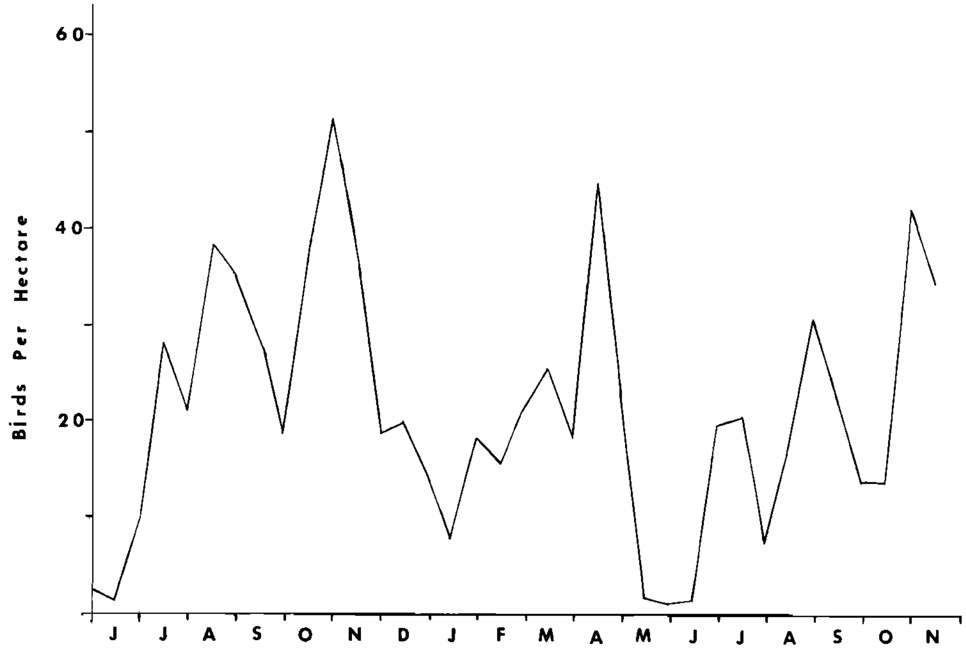

FIGURE 1. Shorebirds per hectare on selected sites in Humboldt Bay, California, from June 1968 to November 1969.

curred along the edges of the pond with bulrush (*Scirpus acutus, S. paludasus*) and willow (*Salix* sp.) in scattered stands.

Most of the censusing was accomplished on small representatives of each habitat type, between two and 20 hectares in size. A census was usually taken on a weekly or biweekly basis, dependent on the tidal sequence. All shorebirds in the area were counted.

During the study nearly 4000 shorebirds were trapped using mist nets and a rocket net (Gerstenberg and Harris 1976). Many were color marked for identification in the field.

RESULTS

Thirty-four species of shorebirds were found using the eight habitats studied at Humboldt Bay (Table 1). Five species were found only once or twice on one habitat. Twenty percent were found on all habitats and 35 percent were found on six or more habitats.

Mud flats were the most heavily utilized habitat in the bay. Use of most other habitats was related to the daily tidal sequence. When the mud flats were exposed, birds were found feeding on them. At high tide when the mud was flooded the birds either roosted near the edge of the bay or moved to alternate habitats. This general pattern varied when tides were exceedingly high, forcing the birds off adjacent sites to alternate habitats or when heavy rains flooded pastures, swelled creeks entering the bay and silted the mud flats, forcing the birds to pastures or out of the area.

Shorebird use of a habitat is related to the number of birds in an area and the availability of the habitat as a feeding or roosting site. Similar to other areas in California, most use of Humboldt Bay is by migrating and wintering shorebirds (Fig. 1). Low numbers and species were found in late May and June (summer)

TABLE 2
FREQUENCY AND DENSITY OF SHOREBIRDS ON MUD FLATS, HUMBOLDT BAY

Species	Frequency			Birds/census/5 ha		
	High[a]	Mid	Low	High	Mid	Low
Black-bellied Plover	62.2	81.6	100.0	10.01	6.10	25.70
Killdeer	8.9	11.8		0.64	0.25	
Black Turnstone	9.6	44.8	44.5	0.40	1.53	2.27
Ruddy Turnstone	7.5	17.6	16.7	0.32	0.57	0.32
Semipalmated Plover	13.0	11.8	11.1	0.94	0.49	0.37
Dunlin	48.0	44.8	44.5	2412.00	741.30	81.30
Western Sandpiper	75.4	33.1	94.4	350.80	15.76	210.80
Least Sandpiper	67.1	21.3	55.6	73.64	7.12	14.63
Sanderling		59.5	5.6		16.48	0.12
Wandering Tattler		8.8			0.07	
Dowitcher (two species)	53.4	39.7	77.8	124.04	6.08	77.59
Greater Yellowlegs	16.4	2.9	16.7	0.82	0.05	0.25
Knot	1.4	5.1	22.2	0.05	0.30	0.82
Marbled Godwit	80.8	90.4	94.4	100.60	29.40	30.64
Willet	79.5	90.4	95.5	13.15	11.71	37.31
Long-billed Curlew	50.7		16.7	2.40		0.25
Whimbrel	6.8	15.4		0.22	0.17	
American Avocet	16.4		5.6	1.63		0.07

[a] High, mid and low refer to intertidal level on mud flats.

when shorebirds used the mud flats almost exclusively. This was due in part to the unavailability of alternate habitats which had dried up or become rank with vegetation. Fall brought an influx of birds beginning in early July. There were several waves of movement due to differential movement by species, age and sex groups. In early fall (July to 15 August) the Short-billed Dowitcher (*Limnodromus griseus*) and Western Sandpiper (*Calidris mauri*) moved through, while in late fall (15 August to 30 November) the Dunlin (*Calidris alpina*) was migrating. Use of alternate habitats increased as they became more available.

From December to mid March (winter) numbers were relatively stable; however, movement out of the area did occur when there was adverse weather. A bird marked in December was seen 350 kilometers south in January after heavy rains occurred. Use of alternate habitats decreased as flooding made the habitats unavailable.

Spring migrants began to arrive in March and moved through the bay until early May. Again there was a series of waves as the spring migrants moved through. Little movement between the north and south ends of the bay occurred except during migration. Few marked birds were seen far from the original place of marking.

Twenty-nine species of shorebirds were recorded on the mud flats (Table 1). Three species, Marbled Godwit (*Limosa fedoa*), Willet (*Catoptrophorus semipalmatus*) and Black-bellied Plover (*Pluvialis squatarola*) were seen on more than 75 percent of the censuses. Average density through the year was 33 birds per hectare. Highest density occurred on 30 April 1969 when 370 birds per hectare were present on a high mud flat and on 14 November 1968 when 307 birds per hectare were present.

Mud flats were separated into three subdivisions according to when the area became exposed in the tidal sequence. High-level mud flats were the first to become exposed and were located near the edge of the bay. Mid-level flats were exposed during most tidal sequences and were located away from the edge of the bay or in areas where the flats were lower in elevation. Low-level flats were fully exposed only on a minus tide.

The Willet, Marbled Godwit and Dunlin showed little preference for any particular level of mud flat (Table 2); however, use of the higher mud flats were more concentrated for the Marbled Godwit and Dunlin. Killdeer (*Charadrius vociferus*) and Whimbrel (*Numenius phaeopus*) were found only on high or mid-level flats. Knots (*Calidris canutus*) were found most often on low level flats.

Sanderlings (*Crocethis alba*) used mud flats adjacent to the sand flats or mud flats which had high sand content. Long-billed Dowitchers (*Limnodromus scolopaceus*) were found on the high-level mud flats feeding in deep channels usually when freshwater areas were not available.

Seasonally the highest number of species, and the highest density (Table 3), were found during fall. The Marbled Godwit was found on mud flats more than 70 percent of the time during all seasons while the Willet occurred similarly except during summer. The Western Sandpiper was most numerous during spring and the Dunlin during late fall and through winter.

The incoming tide forced shorebirds off the mud flats to alternate habitats. Most birds would spend at least some time on the adjacent salt marshes before moving to other areas. Few birds were found using the salt marshes during low tide. As the tide began to recede from high, some birds started feeding in the higher channels which meandered through the marshes. Eight species were seen feeding in such situations. During this time there was an influx of birds moving from other habitats. Mass movement just prior to the exposure of the mud flats occurred regularly.

Sixteen species were recorded roosting on the salt marshes (Table 1), the most frequent the Marbled Godwit and the most numerous the Western Sandpiper. Density on this habitat (330 birds per hectare) was high because the birds were in a small area.

Sand flats occurred in the mid channel and in south bay. Twenty-one species were recorded with the most regular being the Black-bellied Plover, Sanderling, Marbled Godwit and Willet. Sanderling, Dunlin and Western Sandpiper were the most numerous. Density was 26 birds per hectare. Use was most heavy during fall (46 birds per hectare) with less use during winter and spring and almost none during summer (Table 3). Heavy rain during winter caused silting of the flats after which bird use decreased. Sanderlings were in highest numbers from early fall through spring.

Most shorebird use of the tidal slough was on the mud flats exposed along the sides and the bottom. Fourteen species were found with the Willet the most frequent and the Western Sandpiper the most numerous (Table 1). Highest usage occurred during early fall and spring. Ten to 12 species were usually present throughout the year except summer. The most numerous species during fall was the Western Sandpiper and during the spring the Dunlin was the most numerous.

Large numbers of shorebirds, sometimes exceeding 40,000 birds, used the log rafts and pilings along the sides of the slough for roosting at high tide.

TABLE 3
SEASONAL USE (BIRDS/HECTARE) OF EIGHT HABITATS, HUMBOLDT BAY

Season	Mud flat	Sand flat	Tidal slough	Sewage pond	F/W marsh	Upland	Salt marsh	Sand beach
Early Fall	31.03	46.46	47.03	1.82	0.01	0.57	82.60	5.35
Late Fall	47.68	26.54	21.56	55.00	36.01	21.00	389.60	29.77
Winter	32.23	16.69	41.86	0.64	0.91	20.93	512.20	
Spring	46.47	9.50	62.26	15.77	5.48	3.34	124.40	
Summer	2.12	1.40	2.60	0.66	0.01	0.00	1.60	

At high tide species such as the Black-bellied Plover, Killdeer and Least Sandpiper (*Calidris minutilla*) moved directly to upland areas where they were seen feeding in the open pastures or along the edges of marshes or water areas. Other species such as the Short-billed Dowitcher and Dunlin would also move to the uplands but usually only to roost. Heavy use of the uplands did not occur until the first rains had dampened the soil. Use would increase as water saturated the fields causing worms to become exposed. At this time Marbled Godwits would move to the fields.

Twenty species of shorebirds were found in upland areas with the most frequent being the Black-bellied Plover, Killdeer and Greater Yellow-legs (*Tolanus melanoleucus*) (Table 1). The most numerous was the Dunlin. Highest density occurred during winter.

Freshwater marshes occurred throughout the area and shorebird use was related to water content in the marsh and tidal sequence. A marsh was unsuitable for use when flooded or when too little water was present and vegetation was rank. Fourteen species were found in this habitat. The Killdeer nested in suitable marshes and was found throughout the year. Both Common Snipe (*Capella gallinago*) and Killdeer were found on 60 percent of the census (Table 1). The Common Snipe was the most numerous (3.5 birds per 5 hectare) which was very low when compared to other feeding areas. Seasonally the heaviest use was during the spring with little or no use during summer and early fall (Table 3).

A habitat not studied in other coastal areas was the sewage lagoon. It provided roosting sites on dikes and feeding areas along the shore and in the pond. There were 20 species present with the most numerous being the Northern Phalarope (*Lobipes lobatus*) which occurred as a spring and fall migrant. Other species frequently found were the Least and Western sandpipers. The Least Sandpiper used the area as an alternate feeding site and was found over 70 percent of the time. Seasonally the heaviest use occurred during late fall and spring. Little use was found during winter or summer (Table 3).

During the fall of 1969 a small stretch of sand beach was censused. Thirteen species were seen (Table 1) with the Sanderling being found on every census and occurring as the most numerous species. The Least Sandpiper and the Black-bellied Plover were found in largest numbers and the Willet was found on most census in low numbers.

Recher (1966) noted that spring movement was more rapid and movement time more compressed than fall. This caused the population density to be higher in spring than fall. In Humboldt Bay density on mud flats was highest in late fall when Dunlin were moving through the area and late spring when Western Sandpipers were migrating. The overall density on the mud flat was slightly higher in spring than fall and only the tidal slough and freshwater marsh had higher densities in spring. The total population would be higher in the fall than in the spring because winter mortality had taken place.

Recher (1966) also noted that more mud flat was available for longer periods in April and May than in the fall. This would cause the birds to be dispersed more evenly throughout the mud flat. In Humboldt Bay alternate habitats were more available in spring than fall. Winter rains had made marshes and uplands available providing more habitat.

Importance of alternate habitats depended on the individual species needs. The Least Sandpiper appeared always to be feeding. They moved from the mud flat to upland or freshwater marshes, continuing to feed. Other species such as the Marbled Godwit or Dunlin roosted on the salt marsh after feeding and only if the tidal sequence was especially long would they seek alternate feeding sites. During periods of stress the alternate areas became more important, especially during winter storms or spring migration. Thus, although the mud flat is the most important habitat studied, alternate habitats are essential to maintain the shorebird density and species in Humboldt Bay.

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BANDING STUDIES OF MIGRANT SHOREBIRDS IN NORTHWESTERN COSTA RICA

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ABSTRACT.—The coastal shorebird fauna in northwestern Costa Rica was studied over two and a half years at two tidally exposed mud flat sites. Twenty-nine species were recorded and over 1500 individuals of 10 species were banded. Of these three bred locally, and 17 occurred regularly as migrants or winter residents or both. For 11, new distributional data for Costa Rica are reported. Differing patterns of seasonal occurrence are described. Several species showed strong site fidelity. Some data for the Western Sandpiper also suggest strong flock fidelity.

Although the land birds of Costa Rica are well known (Slud 1964 and several later authors), relatively little has been done there on shorebirds. Recent papers that do treat Costa Rican shorebirds (Orians and Paulson 1969, Jehl 1974, Stiles and Smith 1977) deal mainly with new records for the country.

Over the last two and a half years we have conducted a shorebird banding program in northwestern Costa Rica. On each of our regular visits to this area we have recorded numbers of all species present. These data shed new light on the abundances, status, seasonal distribution, and migration schedules of a variety of shorebird species.

STUDY AREA AND METHODS

Our major study site, Salina Bonilla, is located 1.5 km SE of the town of Colorado, Guanacaste Province, Costa Rica. It consists of a series of shallow salt ponds about 5 ha in total area, and is about 0.3 km inland from the Gulf of Nicoya (Pacific Ocean), being connected to it by channels through the intervening mangrove swamp. The salt ponds are separated from each other by mud dikes, and a system of sluices connecting the ponds with one another and with the mangrove swamp permits control of the water level. The water is usually 10–20 cm deep in the smaller ponds, but parts of some larger ponds may be up to 50 cm in depth. Pond bottoms are soft mud, and two areas of mud flats that were regularly exposed were important resting areas for shorebirds for the first 25 months of the study.

In addition, starting in February 1977 we have made observations at Salina La Flor, 3 km W of Salina Bonilla. This salina is slightly larger (8 ha) and closer to the sea (0.1 km), but is otherwise very similar to Salina Bonilla. At low tide extensive mud flats are exposed along the nearby coast, and are the major feeding areas of most of the birds from both salinas. There are no sandy beaches, salt marshes, grassy ponds, or rock outcrops in the immediate vicinity of either salina.

We found that the best way to catch birds for banding was to set mist nets along the dikes to intercept birds flying from the coast into the salinas on the incoming tide. The optimal conditions for this were a high tide around 21:00, such that most birds arrived within 1–2 hours after dusk. Optimal tide conditions thus occurred twice monthly, and we timed our visits accordingly. We usually made censuses either in late afternoons or the following morning. The data reported here were obtained from October 1974 to March 1977.

SPECIES RECORDED AND THEIR STATUS

Twenty-nine shorebird species have been recorded to date at Salinas Bonilla and La Flor. Of these, three are breeding residents, two apparently pass through only on migration, 15 have been recorded all winter in at least one year, with an additional species (Red Knot) almost certainly having wintered 1976–1977 at Sa-

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TABLE 1
General Status of Shorebirds at the Salinas

Species	Status	Recorded in summer
Central American Jacana, *Jacana spinosa*	Breeding resident	(x)
Black-necked Stilt, *Himantopus mexicanus*	Breeding resident	(x)
Am. Golden Plover, *Pluvialis dominica*	Irregular visitor	
Black-bellied Plover, *P. squatarola*	Winter resident	x
Semipal. Plover, *Charadrius semipalmatus*	Winter resident	x
Wilson's Plover, *C. wilsonia*	Breeding resident	(x)
Long-billed Curlew, *Numenius americanus*	Irregular visitor	
Whimbrel, *N. phaeopus*	Winter resident	x
Solitary Sandpiper, *Tringa solitaria*	Irregular visitor	
Greater Yellowlegs, *T. melanoleuca*	Winter resident	
Lesser Yellowlegs, *T. flavipes*	Winter resident	x
Willet, *Catoptrophorus semipalmatus*	Winter resident	x
Spotted Sandpiper, *Actitis macularia*	Winter resident	x
Least Sandpiper, *Calidris minutilla*	Winter resident	
Semipalmated Sandpiper, *C. pusilla*	Winter resident	
Western Sandpiper, *C. mauri*	Winter resident	x
White-rumped Sandpiper, *C. fuscicollis*	Migrant only	
Dunlin, *C. alpina*	Irregular visitor	
Pectoral Sandpiper, *C. melanotos*	Irregular visitor	
Sanderling, *C. alba*	Irregular visitor	
Red Knot, *C. canutus*	Winter resident	
Short-b. Dowitcher, *Limnodromus griseus*	Winter resident	x
Long-b. Dowitcher, *L. scolopaceus*	Winter resident	
Stilt Sandpiper, *Micropalama himantopus*	Winter resident	
Marbled Godwit, *Limosa fedoa*	Irregular visitor	
Surfbird, *Aphriza virgata*	Migrant only	
Ruddy Turnstone, *Arenaria interpres*	Winter resident	
Northern Phalarope, *Phalaropus lobatus*	Irregular visitor	
Wilson's Phalarope, *Steganopus tricolor*	Winter resident	x

lina La Flor (numbers constant from early February through late March); and eight have been recorded only irregularly (Table 1).

The average relative numbers of the 20 regularly occurring species are shown in Table 2. Since we have only biweekly numbers at best, this seems the most useful way to present these data. Most of the regular winter residents show peaks in spring and fall indicating birds passing through. Fall and spring peaks for a given species may be predictably different: for example, Red Knot is more common in spring than in fall, while Wilson's Phalarope is more common in fall than in spring. Of the three breeding residents, one (Wilson's Plover) shows clear peaks in numbers in fall and spring, indicating migrants passing through; one (Black-necked Stilt) increases in numbers during the winter, the additional birds being probably too many to be all young produced in the area, and thus including migrants; and one (Northern Jacana) being apparently totally non-migratory.

Figure 1 presents our numerical data for the three wintering peeps in greater detail. Unfortunately, as we have only biweekly censuses, some peaks in numbers probably were not detected (e.g. probably there was a spring peak of Semipalmated Sandpipers in April 1976 as there was in 1975; also, we have apparently

TABLE 2
AVERAGE RELATIVE NUMBERS[a]

	Month											
Species	A	S	O	N	D	J	F	M	A	M	J	J
Jacana	o	o	o	o	o	o	o	o	o	o	o	o
Blk-n. Stilt	x	xx	xx	xx	xx	xx	xx	xx	xx	x	x	x
Blk-b. Plover	–	xxx	xx	x	x	x	x	xx	xx	x	o	o
Semipal. Plover	x	x	x	x	xx	x	x	x	x	o	o	o
Wilson's Plover	x	xx	xx	xx	x	x	xx	xx	x	x	x	x
Whimbrel	xx	xx	x	x	x	x	x	xx	x	x	x	x
Grr. Yellowlegs	o	o	o	o	o	o	o	o	o	o	–	–
Lssr. Yellowlegs	x	x	x	x	x	x	x	x	x	o	o	o
Willet	xx	xxx	xx	x	x	x	x	xx	x	x	x	x
Spotted Sppr.	x	xx	x	x	x	x	x	x	x	x	o	o
Least Sppr.	x	xx	x	x	x	x	x	x	x	o	–	–
Semipal. Sppr.	xxx	*	*	xxx	xx	xx	xx	xx	x	o	–	–
Western Sppr.	xxx	xxx	*	*	xxx	xxx	xx	xx	xx	o	o	o
White-r. Sppr.	o	–	–	–	–	–	–	–	o	o	–	–
Red Knot	–	o	–	?	?	?	xxx	xxx	x	–	–	–
S-b. Dowitcher	xxx	xxx	xxx	xxx	xx	xx	xx	xxx	xx	xx	o	o
L-b. Dowitcher	–	–	x	x	x	x	x	x	x	–	–	–
Ruddy Turnstone	o	o	x	o	x	o	o	xx	x	o	–	–
Stilt Sppr.	x	x	x	xx	xx	xx	xx	xx	x	o	–	–
Wilson's Phal.	–	o	o	o	o	o	o	o	o	o	o	o

[a] Key to symbols: –, none; o, <50; x, <100; xx, <250; xxx, <500; *, <1000.

missed both spring peaks of westerns, if their spring and fall migratory routes are the same. Nevertheless, certain conclusions can be drawn from these data: even so far from the nesting grounds, spring peaks in numbers are considerably narrower, i.e., more synchronized and rapid, than fall peaks, at least in Semipalmated and presumably in Western Sandpipers. Secondly, in two of the three years, the fall peak of Semipalmated Sandpipers occurred earlier than that of westerns although in 1976 they may have peaked at the same time. Although the data are less clear, the fall peaks of the Least Sandpiper tended to coincide with those of semipalmateds, and precede slightly those of westerns. Recher (1966) found that leasts passed through central California before westerns.

The data in Tables 1 and 2 represent major differences in known status in Costa Rica for 11 species:

Black-necked Stilt: first breeding records for Costa Rica (see Stiles and Smith 1977 for details).

Black-bellied Plover: reported by Slud (1964) to be ". . . seldom met in larger parties . . ." than 2's or 3's in migration, and still rarer in winter. This species is probably common all winter along much of the Costa Rican Pacific coast.

Surfbird: previously recorded only in the fall (Slud 1964); now appears to be a regular early spring migrant as well.

Long-billed Curlew: first Costa Rican records.

White-rumped Sandpiper: first Costa Rican fall records.

Dunlin: first Costa Rican records (Stiles and Smith 1977).

Red Knot: first Costa Rican winter and spring records.

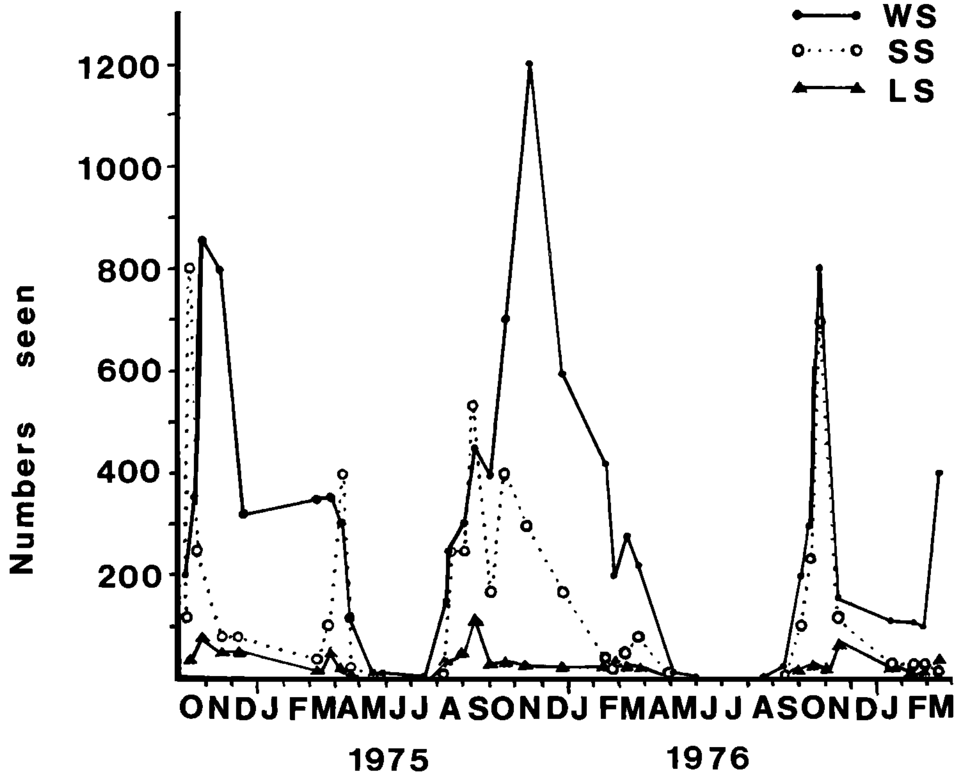

FIGURE 1. Observed numbers of the three wintering peeps: Western Sandpiper (WS), Semipalmated Sandpiper (SS) and Least Sandpiper (LS) in the study area.

Short-billed Dowitcher: Slud (1964) lists this as uncommon both in migration and in winter, being "met singly as a rule" (p 97). Our data indicate that it is locally common to abundant in winter.

Stilt Sandpiper: first recorded in Costa Rica by Orians and Paulson (1969) who found it in both migrations; our data are the first winter records.

Marbled Godwit: first Costa Rican spring records.

Wilson's Phalarope: first Costa Rican records.

TABLE 3
RECOVERIES OF SHOREBIRDS BANDED AT SALINA BONILLA

Species	Total banded	Total recovered	Per cent recovered
Black-bellied Plover	50	—	—
Semipalmated Plover	20	1	5.00
Willet	52	—	—
Spotted Sandpiper	128	14	10.94
Least Sandpiper	45	—	—
Semipalmated Sandpiper	342	7	2.05
Western Sandpiper	696	37	5.32
Red Knot	29	—	—
Short-billed Dowitcher	137	2	1.45
Long-billed Dowitcher	23	—	—

TABLE 4
Timing of Recoveries

Species	Recovered		
	Same winter	1 year later	2 years later
Western Sandpiper	13	21	3
Semipalmated Sandpiper	3	3	1
Spotted Sandpiper	7	6	1
Short-billed Dowitcher	1	—	1
Semipalmated Plover	—	—	1

Finally, individuals of nine migrant species have spent at least one summer at Salina Bonilla; these are birds that failed to go north to breed (Tables 1 and 2). Of these, four were found in only one of the two summers: Spotted Sandpiper, Lesser Yellowlegs, Western Sandpiper, and Wilson's Phalarope. The other five species were present both summers, two of these (Willet and Whimbrel) being present in far greater numbers (40 to 60 birds) than the other three. Since Willets do not breed until they are 2 years old (Palmer 1967), most of the summer Willets are probably yearlings; the same may be true also for Whimbrels.

BANDING RETURNS

To date we have banded 1567 individuals of 21 species at our study area; those species with 20 or more banded individuals are listed in Table 3. Of these, we have recaptured 61 individuals of five species, our highest return rates being for Spotted and Western sandpipers (Table 3). The timing of these returns is analyzed in Table 4. At least one individual from each of the five species was recaptured two years after having been banded.

Several shorebird species thus demonstrate strong site fidelity. Such tradition is well known for breeding sites, and has recently been demonstrated in a wide variety of wintering passerines (Diamond and Smith 1973, Ely 1973, Loftin et al. 1966, Thurber 1972 for Central and South America; Moreau 1969 for Africa). Considerably less is known about site fidelity in wintering shorebirds, although ffrench (1973) reports "numerous" returns on presumably wintering Semipalmated and Western sandpipers, some up to 3 years after banding, in Trinidad.

One of the most surprising aspects of our recapture data is shown in Table 5. On five instances, two or more Western Sandpipers that had been banded at the same time were recaptured together at the same later date. Yet four of the five instances, involving a total of nine birds, were recaptured the following year (i.e.,

TABLE 5
Joint Recoveries of Western Sandpiper

Birds recovered	Band numbers[a]	Date banded	Date recovered	Period
2	05, 11	10-17-76	11-29-76	same winter
2	79, 80	03-08-76	10-02-76	next winter
2	41, 46	02-08-76	10-31-76	next winter
2	66, 70	11-18-74	12-26-75	next winter
3	35, 38	10-28-74	03-09-76	next winter

[a] The last two digits if birds were from the same string of 100 bands.

after one round-trip north). Using the procedure outlined in Appendix I, we have analyzed these data, and find that Western Sandpipers marked on the same date were recaptured together significantly ($P < 0.01$) more often than expected by chance alone.

These data thus strongly suggest that not only site fidelity but also strong flock fidelity exists in migrant and wintering Western Sandpipers. It is even possible that mated pairs may remain together all winter and mate again the following spring. Clearly more data are needed, but the closeness of the band numbers in many cases (Table 5) indicate that this association is indeed a real phenomenon. For example, the two consecutive Western Sandpipers (79 and 80) banded in March 1976 were recaptured in the same net at the same time in October 1976. If this is a widespread phenomenon among wintering shorebirds, it could greatly affect our current understanding of how and when pairs are formed.

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APPENDIX

The following procedure was used to determine whether or not the number of joint recaptures (birds banded on the same date being recaptured together) was greater than could be expected by chance alone:

a) Calculate the probability that 2 random recaptures would involve birds banded on the same date (BSD pair):

$$P_s = \sum_{i=1}^{i=n} \left(\frac{N_i}{N_T}\right)\left(\frac{N_i - 1}{N_T - 1}\right) = .065$$

where N_i = number banded on date i
N_T = total number banded = 696 Western Sandpipers
n = number of banding dates = 26.

b) Calculate the probability that any 2 recaptures would involve birds banded on different dates (BDD pair):

$$p_\alpha = \sum_{i=1}^{i=n} \left(\frac{N_i}{N_T}\right)\left(\frac{N_T - N_i}{N_T - 1}\right) = 1 - p_s = .935$$

c) Data: excluding all singles (only 1 bird recaptured on a date), we have 11 birds involved in BSD recaptures (4 pairs, 1 triple: Table 5) and 20 in BDD recaptures (2 pairs, 3 triples, 1 quadruple). Counting each triple as 3 pairs and each quadruple as 6 pairs (the number of possible 2-bird combinations), we get 7 BSD pairs and 20 BDD pairs (our *observed* data). Expected values, obtained from using the probabilities calculated in a) and b) above, are 1.75 and 25.25, respectively. χ^2 (1 d.f., Yates correction) = 13.78, $P < 0.01$.

Studies in Avian Biology No. 2:49–53, 1979.

NOTES ON CHARADRIIFORMES OF THE SOUTH COAST OF PERU

R. A. HUGHES[1]

ABSTRACT.—On the south coast of Perú, at Mollendo, resident Charadriiformes consist of two oystercatchers, two plovers, four gulls, and three tern species. This fauna is augmented seasonally by 38 species of Nearctic migrants. An additional seven species representing tropical and South American breeders occur irregularly. A second area of coastal wetland habitat occurs 75 miles to the north of Mollendo, but otherwise suitable habitat for shorebirds along this extreme desert coast occurs 300 miles to the north and 800 miles to the south.

With the exception of the Tumbes district in the far north, the Peruvian coast is very arid and under the domination of the Peru Current and its associated upwelling phenomena. Apart from rare years when the warm current "El Niño" affects the region, sea surface temperatures along shore, south of latitude 6°S, remain within the range of 15°–20°C, regardless of season, with higher means offshore. Away from occasional river valleys, the seaboard is backed by waterless deserts.

These general conditions attain their maximum expression along the southern shores of the republic, in the departments of Arequipa, Moquegua and Tacna where, along 400 miles of coastline, there are only two significant areas of wetland habitat. These lie within 75 miles of each other in coastal Arequipa, at Pucchún, near Camaná (16°40′S, 72°50′W) and Mejía, near Mollendo (17°01′S, 72°01′W), close to the mouths of the Majes and Tambo rivers, respectively. For the rest, the whole of this long shore is made up of flat, open and heavily surf-beaten beaches alternating with steep and rocky stretches.

Due to the lack of wetland habitats along so much of the 'Desert Coast' of western South America, an exceptional importance attaches to these isolated areas which, apart from a surprisingly rich and diversified native fauna of such groups as grebes, Ardeids, Rallids and ducks, are also utilized by numerous migrants from the Nearctic Region, especially shorebirds. North of Pucchún the nearest coastal stopping area for most shorebirds is the Pisco Bay district, 300 miles distant, whilst south of Mejía there are no suitable areas as far as the mouth of the Huasco River in southern Atacama, Chile, more than 800 miles away.

At both Pucchún and Mejía there are brackish coastal lagoons, freshwater pools, good stands of typical marshland plants (*Typha, Scirpus,* etc.) with *Distichlis* grasslands on the drier ground. The water level in the lagoons is subject to seasonal variations, being highest between May and August and lowest between October and January, at which time wide mudflats are exposed. These variations are due partly to increased evaporation during the southern spring months and partly to changes in river flow. The volume of the rivers of south coastal Peru falls to its lowest ebb between September and November, the first freshets occurring in December as a result of the onset of the summer rainy season in the Andean interior, the flood season lasting from January to April.

Resident Charadriiformes along the South Coast of Peru are relatively few:

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[1] c/o Casilla 62, Mollendo, Perú.

Haematopus ater (Blackish Oystercatcher).—Occurs all along the coast in small numbers.

Haematopus palliatus (American Oystercatcher).—Very local and uncommon.

Charadrius alexandrinus (Snowy Plover).—Frequent on all lengthy sand beaches.

Charadrius vociferus (Killdeer).—Locally common, chiefly in wetlands or cultivated fields near the sea and consequently limited to the proximity of river valleys.

Larus dominicanus (Kelp Gull).—Frequent all along the seaboard.

Larus belcheri (Band-tailed Gull).—The dominant gull along the rockier stretches of the coast and at the inshore islands.

Larus modestus (Gray Gull).—Very abundant along sand beaches, much less so elsewhere. Despite its abundance, it is not known to breed in Perú and its numbers decline sharply between November and February.

Larus cirrocephalus (Gray-hooded Gull).—Very local and scarce; virtually confined to brackish coastal lagoons.

Sterna hirundinacea (South American Tern).—Very scarce resident, numbers being increased by immigration from the south during the southern winter (April–September). A well-defined but thin southerly movement is perceptible at Mollendo in August.

Sterna lorata (Peruvian Tern).—Breeds on sand beaches in scattered colonies, mainly between October and January. The birds largely disappear from the region between March and July.

Larosterna inca (Inca Tern).—Common all along the coast, especially the rockier sections.

Passing mention should also be made of the curious endemic Peruvian Thickknee (*Burhinus superciliaris*) which, although a bird of the coastal deserts, often descends at night to forage along beaches where halophytic vegetation (*Salicornia*) is well developed, and also of the Least Seedsnipe (*Thinocorus rumicivorus*), a common resident in the '*loma*' fog-vegetation of the coastal hills, small parties of which frequently pay brief visits to the *Salicornia* flats, sometimes pausing to drink at the margins of pools and lagoons.

No less than 38 species of Nearctic Charadriiformes have been recorded from the South Coast of Perú and Table 1 illustrates the relative abundance of each species, the figures being based on actual counts taken in the Mollendo district during the five years between 1971 and 1975.

The fall passage generally becomes apparent as early as the first half of August, reaching a peak in October and November. December and January comprise a relatively quiet period but movements connected with the spring passage become evident in February, increasing notably in March and April, declining rapidly thereafter, although belated birds, by then often in full breeding plumage, may be seen well into May. In June and July Nearctic birds are normally absent from the region apart from isolated individuals which, for any one of various possible reasons, have not returned north in order to complete the breeding cycle. In this respect, the South Coast of Perú differs considerably from the Pisco Bay district, slightly further north, where appreciable numbers of non-breeding shorebirds remain throughout the northern summer months. In the South the species most

TABLE 1

Annual Totals of Nearctic Charadriiformes Recorded at Mollendo, Peru, 1971–1975

Year	1971	1972	1973	1974	1975
Field hours	188	170	181	220	243
Charadrius semipalmatus	39	18	22	70	95
Pluvialis dominica	1	7	9	10	7
Pluvialis squatarola	66	127	126	76	66
Arenaria interpres	194	42	107	68	55
Aphriza virgata	20	6	12	62	41
Calidris alba	23,156	23,581	15,650	18,629	12,512
Calidris canutus	82	–	–	–	3
Calidris melanotos	86	32	38	31	31
Calidris bairdii	294	184	330	907	87
Calidris fuscicollis	–	–	–	–	1
Calidris mauri	1	–	–	12	31
Calidris pusilla	576	376	243	1301	879
Calidris minutilla	–	2	50	129	100
Actitis macularia	33	23	10	15	9
Micropalama himantopus	25	54	1	21	76
Tringa solitaria	–	–	–	1	–
Tringa flavipes	1016	1483	602	754	2555
Tringa melanoleuca	357	592	353	678	1073
Numenius phaeopus	189	217	193	240	329
Catoptrophorus semipalmatus	4	21	4	7	3
Limnodromus griseus	15	–	2	1	28
Limosa haemastica	3	–	4	8	12
Limosa fedoa	–	–	–	–	1
Steganopus tricolor	702	338	682	1033	347
Phalaropus/Lobipes spp.	3	32	157	216	330
Stercorarius parasiticus	56	122	141	155	130
Stercorarius pomarinus	–	–	–	–	2
Sterna hirundo/paradisaea	6366	11,769	13,471	22,375	26,808
Sterna elegans	6300	6529	1076	932	2429
Sterna maxima	–	1	–	1	–
Sterna sandvicensis	–	–	11	40	107
Chlidonias niger	–	8	212	25	242
Gelochelidon nilotica	3	3	31	121	39
Larus pipixcan	39,249	157,033	264,294	78,124	88,663
Larus atricilla	–	–	–	2	4
Xema sabini	–	7	1	2	3

frequently recorded in these months are Whimbrel (*Numenius phaeopus*), Greater Yellowlegs (*Tringa melanoleuca*), Sanderling (*Calidris alba*) and Ruddy Turnstone (*Arenaria interpres*), usually in one's and two's and seldom in greater numbers.

Not all species arrive and depart at the same times, of course, there being many variations to the theme. Some species, such as the Pectoral and Baird's Sandpipers (*Calidris melanotos* and *C. bairdii*) and Wilson's Phalarope (*Steganopus tricolor*) occur primarily during the two passage periods with a hiatus in between; others, like the Sanderling, Greater Yellowlegs, Lesser Yellowlegs (*Tringa flavipes*), Franklin's Gull (*Larus pipixcan*) and Common Tern (*Sterna hirundo*) are abundant "winter" residents as well as passage migrants, although their numbers tend to be highest during the two passage periods. Still others

TABLE 2

AVERAGE MONTHLY COUNTS OF SIX REGULAR MIGRANT SHOREBIRDS AT MOLLENDO, PERU, 1971–1976

Species	J	F	M	A	M	J	J	A	S	O	N	D
Steganopus tricolor	11	8	41	4	5	0	0	49	382	162	3	X[a]
Aphriza virgata	0	0	0	0	0	0	0	19	8	1	X	0
Calidris alba	1299	1579	3094	2520	1705	66	61	815	2525	2925	2711	2992
Tringa flavipes	166	244	593	35	2	0	0	24	36	37	29	42
Numenius phaeopus	4	3	15	11	3	2	2	49	52	82	53	10
Micropalama himantopus	5	0	28	10	X	0	0	1	1	X	X	1

[a] X, present but averaging less than 1.

appear overwhelmingly during only one of the two passage periods: records of the American Golden Plover (*Pluvialis dominica*), Stilt Sandpiper (*Micropalama himantopus*) and Sandwich Tern (*Sterna sandvicensis*) refer mainly to the spring passage (February to April), those of the Surfbird (*Aphriza virgata*), Willet (*Catoptrophorus semipalmatus*) and Sabine's Gull (*Xema sabini*) being concentrated in the months between August and December, i.e., the fall passage.

By referring to Table 1 it can be seen that the majority of listed migrants occur annually; the truly exceptional ones on the South Coast of Peru are Knot (*Calidris canutus*), White-rumped Sandpiper (*C. fuscicollis*) Solitary Sandpiper (*Tringa solitaria*), Marbled Godwit (*Limosa fedoa*), Pomarine Jaeger (*Stercorarius pomarinus*), Royal Tern (*Sterna maxima*) and Laughing Gull (*Larus atricilla*). The normal wintering ranges of these seven species lie either in eastern or northern South America, far removed from our region. The most abundant migrants reaching the region are the Sanderling, both yellowlegs, Wilson's Phalarope, Franklin's Gull, Common and Elegant terns. Sandpiper abundance varies considerably from year to year, this being especially so in the case of the Bairds. Some examples of within-year variability are given in Table 2.

The Nearctic migrants visit all the main habitats afforded by the region but by far the greatest diversity is found on the mudflats around the coastal lagoons, where the birds frequently associate in mixed flocks, encountering no competition from native species apart from the Killdeer. Sand beaches are the preferred habitat of the Sanderling and Willet. Here competition is mainly with the Gray Gull, individuals or pairs of which often chase the Sanderlings in a usually vain attempt to rob them of their food. Visiting Franklin's Gulls also pursue the Sanderlings in the same way. Common, Elegant and Sandwich terns habitually roost on the beaches but they feed over the sea, the first close inshore, the other two mostly favoring deeper water where they suffer considerable harassment by Parasitic Jaegers (*Stercorarius parasiticus*). The rocky stretches of coastline are chosen by the Ruddy Turnstone and Surfbird, which share this environment with Blackish Oystercatchers and the highly specialized furnariid landbird, *Cinclodes nigrofumosus*.

Although each species has its preferred habitat, occasional individuals appear at times in unlikely locations. However, two species are truly catholic in their choice: Franklin's Gull and Whimbrel, these birds appearing almost anywhere.

The pelagic waters are visited by flocks of 'sea' phalaropes (*Phalaropus fuli-*

carius and *Lobipes lobatus*), Arctic Terns (*Sterna paradisaea*) and Sabine's Gulls, none of which is regularly seen from the beaches.

Seven other charadriiform species remain to be considered in the present summary. The Great Skua (*Catharacta skua*) is a regular visitor to the coastal waters from Magellanic South America, appearing chiefly in the southern winter months when the northern jaegers are absent from the region. However, both may be seen at the same time on occasion; the present species tends to victimize larger birds, such as boobies, than its smaller relative. The Tawny-throated Dotterel (*Oreopholus ruficollis*) from southern South America is another winter visitor, appearing in small flocks in coastal farmlands and among the fog-vegetation of the adjacent uplands, avoiding beaches and wetlands alike. The Andean Lapwing (*Vanellus resplendens*) from the Puna Zone of the high Andes is no more than a casual visitor, seen very occasionally at the coastal wetlands. There is no resident population of the Common Stilt (*Himantopus himantopus*), but occasional individuals appear briefly at long intervals at the coastal lagoons. It is of interest to note that such occurrences have involved birds of both the northern '*mexicanus*' and southern '*melanurus*' races, indicating vagrancy from both north and south. The Andean Gull (*Larus serranus*) is a regular visitor from the high Andes, descending to sea level along the Pacific Coast chiefly during the southern winter months. The Swallow-tailed Gull (*Creagrus furcatus*) from the Galapagos Islands ranges southeastwards over the open oceans off the coasts between Ecuador and South Perú, with a number of records as far south as Mollendo.

Finally, mention must be made of the Black Skimmer (*Rynchops nigra*). This bird is often abundant along the South Coast of Perú where, as in Chile, its presence is markedly seasonal, generally arriving from the north in late September or October, building up to a maximum in December and declining afterwards, although sometimes showing a secondary minor peak in March or April. Records for the May–August period are very few. Many of the birds in October–December are brownish immatures. Such a well-defined seasonal pattern would appear to suggest that the birds originate in North America, which supposition is strengthened by the fact that they associate freely with such undoubted Nearctic migrants as Franklin's Gulls, and Common and Elegant terns. However, all the skimmers observed belong to the dark-underwinged '*cinerascens*' race, native along the great river systems of trans-Andean South America, rather than the pale-underwinged North American '*nigra*,' and their precise origin is a complete mystery.

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THE AUTUMNAL MIGRATION OF BAIRD'S SANDPIPER

JOSEPH R. JEHL, JR.[1]

ABSTRACT.—The migratory route of Baird's Sandpiper in autumn has been the object of discussion for decades. The idea that birds migrate southward along the Cordillera to reach wintering grounds in the Andes is not supported by studies based largely on museum specimens.

Migration patterns of adults and juveniles differ markedly. After leaving the arctic in early July adults move southward over a narrow route, mostly through the High Plains. Females migrate slightly earlier than males. The northern prairies of the United States seem to constitute a staging area preparatory to a direct, 4000-mile non-stop flight to northern South America, and ultimately, in some cases, to Patagonia. This movement is extremely rapid; some adults may complete the 9000-mile trip in five weeks. Most adults depart the United States by mid-August; the latest record is 30 August.

The migration of juveniles is far more leisurely. Birds leave the arctic in late July and the peak of fall migration in the United States is reached in mid- to late August; the peak movements into Patagonia are in early October. Though concentrated in the High Plains and western U.S., the migration extends over a broad front, with records from coast to coast in North America. Apparently juveniles move into the southwestern states before migrating to South America; most bypass Middle America.

There is no evidence of wintering in North or Middle America. Its distribution in South America is not confined to mountainous regions, and the importance of the Andes as a wintering range may have been exaggerated.

The annual migration of Baird's Sandpiper (*Calidris bairdii*), from the high arctic to the tip of South America, is one of the most extensive undertaken by any bird. Baird's Sandpiper breeds from northeastern Siberia, through northern Alaska and Canada, to northwestern Greenland. It winters from "the Andes in northern Ecuador . . . and Chile . . . and from southwestern Bolivia south through western Argentina (A.O.U., 1957) to northern Tierra del Fuego (Jehl and Rumboll 1976). Though fairly common in many arctic localities (western Alaska, Bailey 1948; Point Barrow, Pitelka 1974; Victoria Island, Parmelee, Stevens, and Schmidt 1967; Banks Island, Manning, Höhn, and Macpherson 1956; Bylot Island, Drury 1961; but probably not on Ellesmere Island, Parmelee and MacDonald 1960), the species is uncommon to rare over most of the United States in fall. This fact has evoked some interest as to its migration route. Because it has been seen or collected fairly regularly at high altitudes in the Rockies, and in Mexico, and winters in the Andes, some have assumed that "*bairdii* often travels the full length of the treeless backbone of both continents" (Peterson 1961). Others consider that "the main flight seems to be directly south through the MacKenzie Valley and between the Rocky Mountains and the Mississippi River to Mexico and South America, where it probably migrates down the west coast to its winter home" (Bent 1927).

This study was undertaken to determine whether data from museum specimens would clarify aspects of Baird's autumnal migration. My interest was largely prompted by the observation that fall-taken adults were rare or absent in many collections, whereas immatures were usually well represented, which suggested that their routes might differ. Observers with whom I discussed this possibility were unable to provide much additional information; indeed, most were unaware of plumage differences that allow the age classes to be distinguished. Typically, field guides indicate that Baird's differs from other small calidridine sandpipers

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[1] Hubbs-Sea World Research Institute, San Diego, California 92109.

("peeps") in having a scaly back. Juveniles *are* scaly backed, but so are juveniles of *all* calidridines; adults are never so marked. Because of bias in the collections, and because field guide authors prefer to base their work on fresh, unworn (i.e., juvenile) specimens and to neglect the worn (if present) adults, published descriptions and illustrations are often incomplete. As a result, many immature calidridine sandpipers have probably been misidentified as Baird's, and many adult Baird's may have been overlooked.

METHODS

I borrowed specimens of fall-taken birds (ca. 15 June to 30 October) from most of the major museums in the United States and Canada.

When large loans were not feasible, I requested curators to provide data on the age, sex, date, and locality of specimens and provided a photograph (Fig. 1) and description of plumage differences between adults and immatures to insure that specimens were correctly aged; in these cases I requested the loan of all specimens thought to be adult.

Although specimen data provide documentation of age and sex ratios among migrating birds, their use has unavoidable drawbacks. Most notably for this study, museum collections were made largely to document distribution, not to solve biological problems. Collectors rarely worked in one area long enough to sample birds through the course of an entire migratory season. Consequently, age and sex classes that might occur could be entirely unrepresented for some localities. Further, as the intensity of collecting has varied geographically, specimen data do not necessarily provide a reliable index to a species' abundance. This is particularly true in areas where a species is common and, accordingly, receives little attention. Thus, additional distributional information was sought in the major regional literature of the United States, Canada, Middle America, and South America, and from field workers knowledgeable about shorebird migration.

For convenience in analysis North America was divided into five zones: West, Rocky Mountains, Central, Midwest, and East (Table 2).

Plumage characters allow the easy separation of adults from juveniles in fall. Briefly, adults retain the blotchy (never scaly) alternate plumage, which may become extremely worn, until after arriving on the wintering grounds. Molt, if present, is usually slight and confined to the upper body (neck, chest, upper back). Juveniles in early fall are easily recognizable by their fresh, unworn plumage, with the buff-edged dorsal feathers that characterize immature calidridine sandpipers. By late autumn some birds become heavily worn, taking on an adult-like aspect; they can still be distinguished by their relatively unworn remiges, especially the buff-edged tertials. Further details on molt are given in Appendix I.

RESULTS

MIGRATION IN NORTH AND MIDDLE AMERICA

Adults.—Most species of calidridine sandpipers are monogamous, with males and females sharing incubation duties. Typically, both parents stay with the brood for a week or so, but the female soon departs, leaving the male to remain with the chicks until they have fledged. Although this pattern has not been firmly established for Baird's Sandpiper from studies on the nesting grounds (Dixon 1917, Parmelee, Stevens, and Schmidt 1967, Pitelka, Holmes, and Maclean 1974), it is supported by specimen data which show that females migrate earlier than males (Table 1). This pattern is somewhat obscured when data from the entire United States and Canada are combined, but is evident among large samples from specific localities (e.g., Colorado, Saskatchewan), and is also shown by the earlier arrival dates of females in South America.

Adults begin to leave the western arctic by late June and early July (Parmelee et al. 1967) and start to appear in southern Canada and the northern United States shortly thereafter (earliest 7 July; Table 2). The brief interval between departure

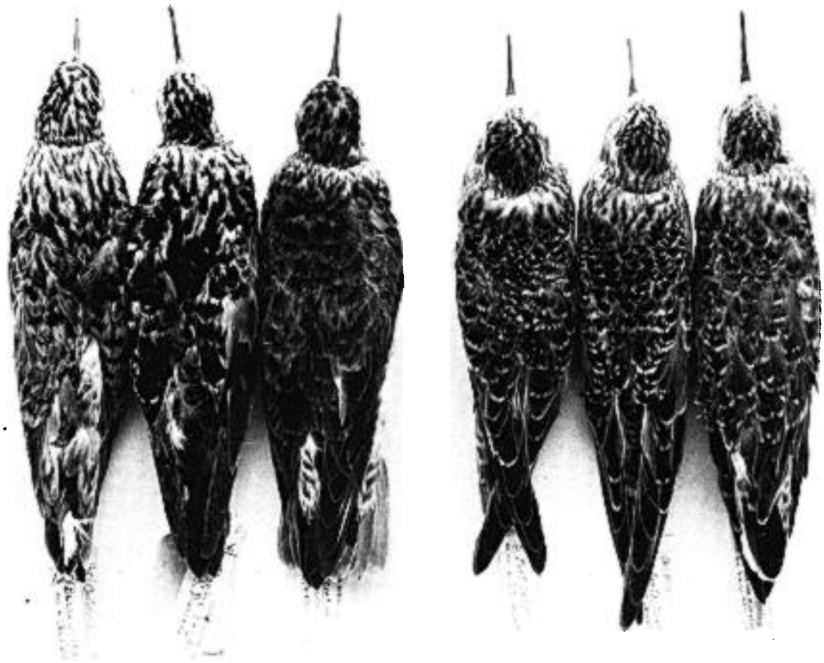

FIGURE 1. Plumage differences between adult and juvenile Baird's Sandpipers. Adults (3 left); Barrow, Alaska, 1 June 1928; Barrow, Alaska, 24 June 1930, Tierra del Fuego, Argentina, 4 November 1973. Juveniles (3 right): Curry Co., Oregon, 22 August 1933; Tillamook Co., Oregon, 11 August 1929; Santa Clara Co., California, 4 September 1937.

and arrival dates virtually requires that most of this distance (ca. 2000 miles from southern Victoria Island to northern North Dakota) be traversed in a non-stop flight.

Considering the breadth of the breeding range, the migratory route of adults is

TABLE 1

Differential Migration Dates for Adult Baird's Sandpipers in Autumn

Date	Saskatchewan		Colorado		All North America			South America[a]	
	♀	♂	♀	♂	♀	♂	% ♀	♀	♂
1–10 July	1?[b]	–	1	–	1 (2?)	1	50	–	–
11–20 July	8	4	2	–	13	7	67	–	–
21–31 July	5	2	2	1	16	10	61	2[c]	0
1–10 August	1	6	–	2 (3?)	10	13 (14?)	43	4	0
11–20 August	–	–	–	2	1	7	12	2	0
21–31 August	–	–	–	1	1	3	25	8	1[d]
1–10 September	–	–	–	–	–	–	–	5	2
10–20 September	–	–	–	–	–	–	–	3	3

[a] Specimens from Peru, Bolivia, Argentina.

[b] Question marks indicate specimens of undetermined sex.

[c] Earliest 29 July.

[d] Earliest 12 August.

TABLE 2

Dates of Baird's Sandpiper Migration in North America and Middle America[a]

	Adult females		Adult males		Immatures	
Locality	N	Dates	N	Dates	N	Dates
WEST						
British Columbia			1	29 July	48	24 July–27 Oct. *24 Aug.*
Washington	3	8–25 July	1	17 July	41	26 July–29 Sept. *30 Aug.*
Oregon					38	23 July–9 Sept. *16 Aug.*
Nevada					6	10 Aug.–14 Sept. *25 Aug.*
California					62	31 July–6 Oct. *1 Sept.*
Hawaiian Is.					3	23 Aug.–6 Sept. *2 Sept.*
ROCKY MOUNTAINS						
Alberta	2	12–17 July	5	10–31 July, 21 Aug. *24 July*	37	27 July–11 Sept., 6 Nov. *20 Aug.*
Saskatchewan	14	17 July–1 Aug. *25 July*	12	17 July–4 Aug. *26 July*	5	1 Aug.–20 Aug. *6 Aug.*
Idaho	1	15 July	1	19 July	44	20 July–9 Oct. *24 Aug.*
Montana					1	7 Oct.
Wyoming			1	27 Aug.	3	15–25 Aug. *20 Aug.*
Colorado	5	7–29 July *20 July*	6	31 July–23 Aug. *10 Aug.*	49	9 Aug.–27 Sept., 20 Oct. *27 Aug.*
Utah			2	6 Aug.	7	19 July–12 Sept., 3 Oct. *23 Aug.*
Arizona	4	3–15 Aug. *9 Aug.*	2	31 July–3 Aug. *1 Aug.*	20	12 Aug.–12 Sept., 18 Nov. *26 Aug.*
New Mexico	1	23 July	1	29 July	12	20 Aug.–11 Sept., 2 Oct. (2) *3 Sept.*
CENTRAL						
Manitoba	2(3?)	12 July–7 Aug. *24 July*	7	26 July–26 Aug. *11 Aug.*	3	5–7 Sept. *6 Sept.*
No. Dakota	8	12 July–25 Aug. *31 July*	8	18 July–10 Aug. *2 Aug.*	17	2 Aug.–9 Sept. *25 Aug.*
Minnesota					14	16 July–19 Sept. *27 Aug.*
Nebraska	1	22 July			6	30 Aug.–13 Oct. *18 Sept.*
Kansas	1	22 July	1	30 Aug.	1	5 Sept.
Oklahoma			3	11–16 Aug. *14 Aug.*	5	21 Sept.–13 Oct. *27 Sept.*
Texas	1	8 Aug.	1	8 Aug.	2	11 Aug., 3 Oct.

TABLE 2. (CONTINUED)

	Adult females		Adult males		Immatures	
Locality	N	Dates	N	Dates	N	Dates
MIDWEST						
Wisconsin			1	14 Aug.	14	15 Aug.–20 Sept. *2 Sept.*
Michigan			(2)	4–15 Aug.	43	13 Aug.–29 Sept. *1 Sept.*
Illinois					4	8–30 Aug. *22 Aug.*
Indiana					8	19 Aug.–6 Sept. *28 Aug.*
Kentucky					1	29 Sept.
Tennessee					1	9 Sept.
Louisiana					3	15 Sept.–9 Nov. *18 Oct.*
EAST						
Newfoundland					1	14 Sept.
Ontario					23	8 Aug.–26 Sept., 7 Oct. *28 Aug.*
Quebec					5	13–24 Aug. *19 Aug.*
Massachusetts[b]						28 July–18 Oct. *mid-Aug.*
Rhode Island					1	17 Sept.
Connecticut					2	14 Sept., 19 Oct.
New York					16	14 Aug.–22 Sept., 30 Oct. *30 Aug.*
Pennsylvania					10	24 Aug.–16 Sept., 2 Nov. *5 Sept.*
Virginia					3	3 Sept.–23 Oct. *25 Sept.*
North Carolina					1	1 Sept.
Bermuda					1	6 Sept.
Florida					1	5 Sept.
MIDDLE AMERICA						
Mexico	9	28 July–13 Aug.	1	6 Aug.	10	6 Aug.–7 Nov.[c]
El Salvador			1	19 Aug.		
Costa Rica			1	4 Sept.[d]	4	25 Sept.–18 Oct.
Panama						19 Sept.–28 Oct.[e]

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[a] Except where noted, this table is based entirely upon museum specimens. Mean arrival dates are given in italics.

[b] No specimens from Massachusetts were examined. Data from Griscom and Snyder 1955. Note, one exceptionally early migrant, 28 July, may be an adult.

[c] Includes two photographed in Baja California on 6 Aug. 1977 (L. Kiff and K. Axelson).

[d] Cocos Is.

[e] From Wetmore 1965: see also Ridgely 1976; age inferred from dates.

extremely narrow. They avoid coastal areas and funnel southward along a route that generally parallels the Rocky Mountains. Of 99 adult specimens examined, 91 were from the Rocky Mountain and Central zones, 5 from the West, and 3 from the Midwest. None was found in the East, although a Massachusetts specimen taken on 28 July (Griscom and Snyder 1955, specimen not seen) is suspect on the basis of date.

There are many records for high altitude localities, but little data to indicate that any significant number actually move along the Rockies. Rather, maximum abundance is achieved in the High Plains. Regional authors (Bailey and Niedrach 1965, Johnston 1960, Sutton 1967, Obserholser 1974) agree that the species is far commoner in eastern Colorado and in western Kansas, Oklahoma, and Texas, than elsewhere in those states. Large numbers of Baird's of unknown age may also occur in the Great Basin (e.g., 8000 at Bear River, Utah, in August 1975), though these movements seem to be irregular (W. H. Behle, pers. comm.).

The movement of adults through southern Canada and the entire United States is extremely rapid. Specimen dates extend from 7 July (Colorado) to 30 August (Kansas), but the bulk of the migration is completed in a matter of several weeks; adult females arrive in the second week of July and virtually disappear from North America by 10 August; adult males appear in the latter third of July and nearly all have departed by 20 August. Banding data from central Kansas show a similar pattern, adults being present from early July to late August, with the peak movements between 1 and 15 August (Ed Martinez, pers. comm.).

Evidently the large prairie region bounded approximately by eastern Alberta, western Manitoba, central Colorado, and central Kansas is the first stop in the migration of adults. Apparently this region is a major staging area and on leaving it most adults fly non-stop to the Andes of northern South America, some 4000 miles distant. A few may move through the southern United States and into northern Mexico, but the numbers involved are not large (Fig. 2). It seems extremely unlikely that the birds follow the Cordillera. These conclusions are based on several lines of evidence.

1. The regional literature indicates that Baird's Sandpipers are commoner in the northern United States than farther south. This information is equivocal because authors have consistently failed to differentiate age classes. However, approximately 75% of the adult specimens were taken north of 40°N (the latitude of central Kansas). While some collecting bias is probable, the adult/juvenile ratio (Table 2) also indicates a relatively higher proportion of adults in the north and suggests, therefore, that adults bypass more southern regions.
2. Early and mean arrival dates of adults in the southern U.S. average later than in the north, indicating that birds reaching this region have made a previous stop.
3. The period during which adults are present in the United States is so brief that there seems insufficient time for a leisurely southward movement.
4. Baird's Sandpiper is very uncommon in Middle America, having been reported from Mexico, Guatemala, El Salvador, Costa Rica, and Panama (Eisenmann 1955, Dickey and van Rossem 1938, Slud 1964, Wetmore 1965, Ridgely 1976, Land 1970, Russell 1964, Monroe 1968, Blake 1950, Friedmann, Griscom, and Moore 1950). Year-round observations at high altitudes in Guatemala failed to reveal its presence (Baepler 1962) and the only records for that country (Dick-

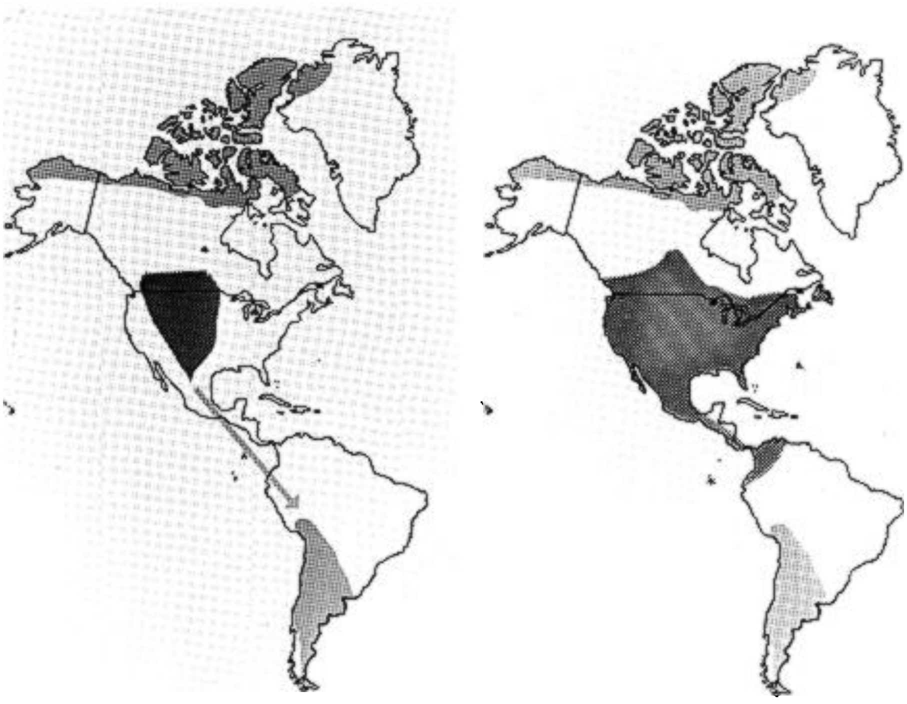

FIGURE 2. The distribution of adult (left) and juvenile (right) Baird's Sandpipers during fall migration as shown by specimen records (cross-hatched). Breeding and wintering ranges (gray) are from A.O.U. 1957, Godfrey 1966, and Meyer de Schauensee 1966. The arrow approximates a great circle route from northern Mexico to the Andes of southern Peru. Distributional records for adults in northern South America are not plotted.

erman 1977) are of three spring migrants at a coastal locality. In Mexico adults and juveniles seem equally common; all of the adults were taken at high altitudes (7000–14,500 feet) in inland localities (meadows in pine woodlands, riparian situations, the lake in the crater of a volcano). Only two fall adults have been taken farther south in Middle America, at Lake Olomega, El Salvador (elev. 2000 feet), and Cocos Island, Costa Rica. Although Cocos Island is 600 miles west of the mainland, it lies on a great circle route between northern Mexico and northern Peru. If a substantial number of birds utilized this overwater route, it would explain the virtual absence of adults (and the rarity of the species) in southern Middle America.

5. Arrival times in South America seem to correspond to the period in which emigrations from the U.S. are indicated. The data are scanty and must be interpreted with caution. Nevertheless, adult females appear so early (29 July, Perú; 10 August, Buenos Aires Province, Argentina) that a direct flight is indicated. Museum specimens of adult males are too rare for analysis; the earliest known to me is 31 August (Perú).

Arrival dates of adults in the southern parts of the Rocky Mountain and Central Zones, and in Middle America (Table 2), also seem to correspond to departure

TABLE 3
WEIGHTS (g) OF FALL-MIGRATING BAIRD'S SANDPIPERS

	Adult males		Adult females		Juveniles	
Area	N	Range and mean	N	Range and mean	N	Range and mean
Northern Alaska	26	34.5–46.8 (38.2)	5[a]	40.5–53.5 (47.3)		
Canada/U.S.	3	38.4–63.1 (49.3)	3	37.0–46.9 (41.9)	32	28.8–60.3 (39.0)
Mexico	1	44.7	3	37.2–47.2 (41.4)	1	27.5
Peru/Argentina/Bolivia			5	32.0–44.2 (37.3)	8[b]	29.5–43.0 (35.2)

[a] Excluding laying females; Museum of Vertebrate Zoology specimens.
[b] Includes six specimens of undetermined age.

periods from the northern U.S., which suggests that migrants with insufficient fat reserves drop out along the route before continuing to the wintering grounds.

6. Weight data, though scanty (see below), are consistent with the interpretation that adults are fully capable of making an extended non-stop migration.

Juveniles.—The migration of juveniles begins in late July (earliest 16 July, Minnesota; 19 July, Utah) and is largely completed by mid- to late September. Migration proceeds over a broad front, with birds moving nonstop from the breeding grounds to southern Canada and the northern United States. Peak arrival times, in the last third of August, correspond to the period when young disappear from arctic localities (cf. Parmelee et al. 1967).

The distribution of juveniles is less circumscribed than that of adults, extending from coast to coast; a few occur west to Hawaii (and beyond to the Pacific islands) and others east to Bermuda. Although specimen records suggest that juveniles are concentrated in the western United States (35% of specimens from the West, 32% Rocky Mountain, 9% Central, 13% Midwest, 11% East), collecting bias is obvious. The regional literature clearly shows that maximum numbers are encountered in mid-continent and that the species is uncommon to rare on both coasts.

The migration period is much more protracted than that of adults. Dates in Alberta, for example, span over six weeks, and along the west coast, where equable weather conditions persist late into the fall, may extend over two months or more. The later mean and early arrival dates in the southern part of each zone are further evidence for a protracted movement. This slower, broader movement in part accounts for the fact that among fall-taken specimens, juveniles are more than five times commoner than adults.

After leaving the northern United States a few young birds may move directly to South America, as indicated by very early arrival dates in Bolivia (25 August) and northern Argentina (14 September). However, the peak arrival of immatures on the wintering grounds does not occur until late September or early October. I suspect that the majority move through mid-continent to the southwestern states or northern Mexico before moving on. The species is common in Texas and Arizona in late summer and early fall (Oberholser 1974, Phillips et al. 1964); and at these periods only juveniles would be expected. Apparently they linger in the southwest until mid- or late September, then fly non-stop to northern South America. There is no evidence that any significant numbers pass through southeastern United States.

Although recorded from México to Panamá, juveniles are rare in Middle America. Indeed, dates of occurrence in Costa Rica and Panama (Table 2) average so much later than departure dates from the United States that birds occurring in the region are probably stragglers, rather than components of the main flight. It is also worth noting that Middle American records of immatures are from coastal as well as inland localities, again showing their tendency to adhere less closely to a well-defined route. As with the adults, there is no evidence to support the idea of a major movement along the Cordillera.

Migration in South America

Data from South America are few. Evidently adults and immatures make their first stop in the northern mountains prior to dispersing to mountain and coastal areas farther south; the species is virtually unreported from the northeastern part of the continent.

As elsewhere, the route taken by adults is narrower than that of the juveniles. All of the adults that I have examined from Ecuador, Perú and Bolivia were obtained at high inland localities; the northernmost coastal records are Buenos Aires, Argentina and Valparaiso, Chile. There are coastal records of juveniles and suspected juveniles in northern South America: these include a specimen from the Galapagos Islands; several sight records from the lowlands of Venezuela in late October (Wetmore, 1939), when only juveniles would be expected to occur; and records for the coast of southern Perú "mostly in September and October . . . sometimes . . . in large flocks" (Hughes 1970).

Adults begin to arrive in late July (earliest 29 July, Perú) and by mid- to late August are fairly common along the Atlantic coast as far south as Rio Gallegos, Argentina. Presumably they reach Tierra del Fuego by early September but critical observations for this period are lacking (Humphrey et al. 1970). Juveniles begin to appear in late August in the north, with peak migration occurring in late September. The migration remains more leisurely than that of the adults, as illustrated by 22 specimens from Argentina (the largest sample available) taken between 10 August and 24 October: only two are immature (14 September and 24 October). Jehl and Rumboll (1976) observed Baird's arriving in Tierra del Fuego into early November, and I suspect that these movements largely comprised immatures.

Weight and Migration

The earliest adult Baird's Sandpiper to arrive in the United States (7 July) presumably left the breeding grounds two days previously; the earliest arrival in Patagonia (Rio Gallegos, Argentina) was taken on 12 August. If some adults are able to complete this 9000-mile trip in as little as 5 weeks, they must average 260 miles a day; and since migration is not continuous, they must undertake at least one non-stop flight of greater extent to maintain this rate. Weight data bearing on this problem are summarized in Table 3.

As with other arctic waders (e.g., *Calidris melanotos*, Pitelka 1959; *C. minutilla*, *C. alpina*, Yarbrough 1970) Baird's lay on few fat reserves prior to leaving the arctic. Females from northern Alaska average only 7 to 10 g heavier than those newly-arrived in the United States, but those reserves are evidently adequate to power the first 2000-mile leg of the journey.

Adults newly arrived in the United States and Mexico range from 37–40 g; juveniles are lighter, averaging 30–35 g. In both groups the heaviest birds weigh approximately twice as much as the lightest (adult range 32–63.1 g; juveniles 27.5–60.3 g), the difference being largely due to fat deposits. In both groups the heaviest birds were taken in the United States relatively late in the migration period, and the lightest, on the average, were obtained in South America. I infer that adults migrate until dropping to a weight of ca. 40 g (juveniles somewhat less), then stop and lay on heavy fat reserves (15–20 g) before continuing.

According to equations proposed by Raveling and LeFebvre (1959) a 50 g sandpiper carrying 15 g of metabolizable fat and flying at 50 mph (McNeil and Cadieux 1972) is capable of a 4400-mile flight. This is more than sufficient to carry a bird from the northern prairies to the northern Andes. That Baird's is capable of such extended flights is evidenced by its occurrence in Hawaii and Austraila (Smith and Swindley 1975). Indeed, a 4000-mile range may be low, as one immature from Hawaii weighing 56 g had nearly 19 g of subcutaneous fat.

At an average speed of 50 mph, 180 hours (7½ days) of flight time are needed for the entire migration. Allowing two stops of 10–14 days to replenish energy reserves (cf. Thomas and Dartnall 1971b, for *Calidris ferruginea*), one in the High Plains and one in northern South America, the minimum travel time would approximate 28 to 36 days. This estimate agrees well with the minimum 5-week (36-day) period suggested by specimen data.

DISTRIBUTION IN WINTER

Although an analysis of winter distribution is beyond the scope of this paper, some comments are warranted. Baird's Sandpiper does not winter in significant numbers except in South America, the major wintering area extending from Perú to northern Tierra del Fuego. The species is commoner in eastern Argentina than has been acknowledged (e.g., Johnson 1965, Jehl and Rumboll 1976, J. P. Myers, pers. comm.), and Howell (1975) has recently shown that it winters abundantly in the deserts in northern Chile, wherever suitable bodies of water are present. Further studies should reveal whether the importance of the Andes as a wintering area has been overemphasized.

According to the A.O.U. (1957) the winter range extends "rarely north to El Salvador, Costa Rica, and Panama," but I find no evidence for that. The only El Salvador record is for August (!) and the species is unknown in Middle America after late October (Slud 1964, Wetmore 1965, Ridgely 1976).

Wintering in North America is even less likely, although a few may manage to survive late into the year (e.g., 6 November, Alberta; Table 2). The latest specimen records are 18 November (Arizona) and 5 December (Colorado). (A Colorado specimen allegedly taken on 2 January [Bailey and Niedrach 1965] is an adult male in full breeding plumage; I cannot credit the data.) Winter sight records have been published for Colorado (Bailey and Niedrach 1965), Texas (Oberholser 1974), and Oklahoma (Sutton 1967); I find them unconvincing and in need of review by local authorities.

Since the mid-1950's, Baird's Sandpiper has been reported almost annually on Christmas Bird Counts in the United States, though none seem to have been authenticated by photographs, specimens, or even subsequent observation by experienced observers. In 1975 for example, 500 (!) were reported (without details) at Laguna Atascosa, Texas. And at Coos Bay, Oregon, 7 were reported along with 5 Whimbrels (*Numenius phaeopus*) and 13 Wandering Tattlers (*Heteroscelus incanum*); an anonymous reviewer (American Birds 30(2):178) noted that "better details were wanting *on the tattlers*" (italics mine). I am convinced that the incomplete field guide treatment, along with a general ignorance of the species' distributional pattern, has played an important role in the submission of these uncritical and probably erroneous reports.

CONCLUDING REMARKS

Nearly seven decades after W. W. Cooke published his studies on shorebird migration, the major features of Baird's Sandpiper's autumn migration have been inferred here with some confidence largely on the basis of museum specimens, most of which have been available for many years. Similar life history data, which are essential for sound conservation programs, could also be reconstructed for many other species from existing specimen material. Unfortunately, the time required to seek out these specimens, arrange for loans, and collect and interpret data, is probably no less than in Cooke's time. The instigation of a national inventory of museum holdings—as important as an inventory of living resources—would help investigators determine whether a biological problem might be profitably attacked at the current time, or whether additional specimen material was needed. This inventory would have other benefits, not the least of which is aiding collection managers in planning for future needs. Lacking such a system, we must accept that many decades more may pass before problems that are currently resolvable or definable can even be approached efficiently. Such ought not be the pace of science in the 20th century.

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APPENDIX: NOTES ON MOLT

PRE-BASIC MOLT

Adults.—Breeding birds become heavily worn by mid-June. At Barrow, Alaska (specimens in San Diego Natural History Museum), light molt may commence in late June, with new feathers appearing on the head, throat, neck, chest, and upper back. By early July, a few birds also show molt on the flanks and abdomen as well. On Ellesmere Island, Parmelee and MacDonald (1960) reported that the pre-basic molt "is well under way . . . by mid-July." The extent of molt on the breeding grounds seems variable, with most of the pre-basic molt taking place on the wintering grounds (Pitelka 1959).

Apparently molt is arrested during migration, as has been reported in many shorebirds (e.g., Holmes 1966, Pienkowski et al. 1976). All but two of the adults I examined from southern Canada and the United States showed little, if any, active molt, and retained enough of the alternate plumage to be easily recognized as post-breeding birds. The exceptions (Oklahoma, 11 August; Colorado, 25 August) appeared to have almost completed body molt.

Body molt is resumed after birds arrive in South America. The timing and sequence is hard to follow because of a lack of material and because a combination of wear and molt makes it difficult to distinguish adults from immatures by late October. Nevertheless, by mid-October most adults seem to have acquired the uniform drab brown basic plumage. Some birds (age uncertain) continue to show light molt on the tail, back, chest, and abdomen into January.

Molt of the primaries extends from late October (earliest 20 October) to mid-January; one specimen taken on 2 February had not yet replaced the outer two primaries. The tertials and scapulars seem to be replaced by early January. Two birds taken in early February were molting rectrices; tail molt seems to be completed by late March or early April.

Juveniles.—The pre-basic molt pattern of juvenile calidridine sandpipers seems related to the length of the migration. Short-distance migrants (e.g., *C. alpina*, Holmes 1966) do not replace the flight feathers, whereas long-distance migrants (*C. ruficollis, C. ferruginea, C. minuta*; Middlemiss 1961; Thomas and Dartnall 1971a, 1971b) replace the entire feather coat. Baird's Sandpipers fall into the latter group.

Migrating juveniles from Canada and the United States show no evidence of molt. By October, many are heavily abraded and have lost the scaly edgings to the dorsal feathers, but they may still be aged accurately by their unworn tertials and remiges.

Molt commences after juveniles arrive in South America, and by late October or early November is usually evident on the upper back, chest, abdomen and scaplars (one bird). A juvenile collected on 24 October had already replaced the entire crown, back, and scaplars, and was missing the inner 2–3 primaries. Another taken on 31 December had replaced the entire body plumage, wing coverts, and all but the outermost primary; the central rectrices had also been replaced. In some birds, body molt is still evident into January. One specimen taken in "January" showed no evidence of primary molt.

PRE-ALTERNATE MOLT

No attempt was made to study the pre-alternate molt in detail, as few spring-taken specimens from the wintering grounds were encountered. Body molt resumes in early spring. Several birds taken in late March and early April showed extensive molt on the back and one bird (Peru, 31 March) appeared to have completed the molt. I suspect that most birds finish molting while en route to the breeding grounds.

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MOVEMENTS AND HABITAT USE BY WINTERING POPULATIONS OF WILLETS AND MARBLED GODWITS

PAUL R. KELLY AND HOWARD L. COGSWELL[1]

ABSTRACT.—A study in tidal habitats of South San Francisco Bay, California, of a group of Willets and Marbled Godwits marked for sight recognition of individuals has provided the first data on local and migratory movements of individuals of these species on the wintering grounds. For the local population as a whole, information was also gathered on population numbers, habitat use and behavior in response to tides, seasons and weather.

The local population was found to roost habitually on an island in a salt marsh during high tides and to feed on a nearby tidal mud flat during low tides. Census data from a tidal mud flat plot showed peaks in numbers of Willets (October) and Marbled Godwits (December) and, when compared to peaks observed in other parts of coastal California, suggested a southward movement of both species through the state during the fall and winter.

Observations of tagged Willets and Marbled Godwits showed the following: Individual birds habitually used certain roosts and feeding areas. A very limited amount of exchange occurred between the habitual roosts and feeding areas and other roosts and feeding areas. The usual distance traveled (one-way) between roosts and feeding areas was about 1000 m. Some Willets were independent of the tidal mud flat and habitually used certain small areas of salt marsh. Sightings of marked Marbled Godwits from inland areas indicate the possibility of a migration on a north-northeast heading from Palo Alto to breeding sites in southern Alberta. Sixty-five percent of the Willets and 35% of the Marbled Godwits returned to the study area (presumably after migrating) long before and independent of the fall migration population peaks. The population peaks probably represent a southward movement of juveniles. The mean interval of absence of marked birds from the study area was 117 days for Willets and 140 days for Marbled Godwits resulting, in most instances, in an eight- to nine-month residence on the wintering grounds. The marked birds exhibited a restricted home range and long-term residence in the study area.

Most shorebirds are highly migratory and their presence in California, a major wintering area, is seasonal. Typically, more than two-thirds of the year may be spent on the wintering grounds. In California, the marine littoral zone, including the shores of the open coast, bays, sloughs and marshes, provides the most extensive habitats utilized. The seasonal occurrence, habitat use, behavior and ecological relationships among migrant and wintering waders have been investigated but, in the absence of marked birds, details regarding local and migratory movements are scarce.

Recently some information has been obtained on local movements of small scolopacids because of the relative ease with which they can be captured and color-banded. Larger scolopacids such as the Willet, *Catoptrophorus semipalmatus,* and the Marbled Godwit, *Limosa fedoa,* although common, are rarely captured and previously have never been marked for sight recognition of individuals. Only one investigator (Luther 1968) has examined the local movements of Marbled Godwits by observing flights between feeding grounds and high tide roosts and seasonal fluctuations in their numbers. Although such studies of unmarked birds do yield data on movements, they inevitably neglect exchanges of birds among wintering populations and the seasonally changing proportion of birds present for a period of time versus those moving through.

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Accordingly, the objectives of the present study were to determine local movements and some aspects of the migratory movements of a group of individually tagged Willets and Marbled Godwits, and to gather information on their numbers, habitat use, and behavior in response to tides, seasons and weather.

STUDY AREA

The study was conducted primarily on the west side of the southern section of San Francisco Bay (Fig. 1) within about 6 km of shoreline from the Dumbarton Bridge on the north to the Palo Alto Harbor on the south. This area consists of extensive tidal mud flats, salt marshes, solar evaporating ponds being used in salt production, and salt ponds not in use, in which rain water accumulates. A golf course lies just inland from a small airport adjacent to the main marsh and a flood control basin with variable ponds is located to the south of the harbor area.

Willets and Marbled Godwits obtain most of their food from mud flats available to them periodically. Storer (1951) has described the tidal rhythms of San Francisco Bay. Luther (1968) has described the main times of movements of Marbled Godwits in relation to tidal cycles.

The salt marshes within the study area amount to about 320 ha and were an important part of it. The Palo Alto salt marsh itself is composed of about 200 ha of cord grass (*Spartina foliosa*) which grows at tide levels from +4 to +5.5 ft above mean lower low water. Pickleweed (*Salicornia virginica*) covers about 120 ha and grows above the +5.5-ft level. Salt grass (*Distichlis spicata*), gum plant (*Grindelia cuneifolia*), and salt bush (*Atriplex* spp.) are also common in the upper levels of the marsh.

Salt pond dikes, varying in height and width, serve as retaining walls and often border San Francisco Bay itself. The salt pond dikes north of Cooley Landing and in other parts of San Francisco Bay are of importance to shorebirds where the salt marsh has been destroyed (Luther 1968).

The mouth of San Francisquito Creek and to a lesser extent the mouth of the Palo Alto sewage outfall served as important feeding areas on the mud flat, presumably because of detritus and nutrient enrichment at these points. The Pacific Gas and Electric Company boardwalks, installed for maintaining the power poles which border the bay, provided access for observers to areas of the salt marsh and tidal mud flat. The nearby golf course, adjacent fields and the ponds of the flood-control basin were of occasional importance during the study.

METHODS

More than 200 h were spent by the first author in field observation from November 1972 to May 1974. Data were taken during all seasons, at all times of the tidal cycle, during all weather conditions, and at all times of the day. However, data from only two nights and only five rainy days were obtained due to insufficient light or interference with optical instruments. During the 17-month study, observations made on 147 different days were usually coordinated with the tidal cycle.

The sites of most observations were the Pacific Gas and Electric (PG&E) boardwalk along the bay in Palo Alto and south of Cooley Landing, and the dikes bordering the Palo Alto salt marsh.

Willets and Marbled Godwits were counted on a mud flat census plot (Fig. 1) and at high tide roosts. Peak departure flight times, peak arrival flight times, tide levels, habitat use and weather conditions were recorded.

Tidal mud flat census methods have been reviewed by Storer (1951), Jehl (1963), Recher (1966), and Gerstenberg (1972). Storer (1951) censused a mud flat when the maximum number of shorebirds were feeding and before the birds got too far away from the high tide mark to be identified. He considered that these conditions were met when the tide was one-third to one-half ebbed, finding that as the tide reached its lowest ebb and the birds had obtained sufficient food, they began to fly about on the mud flat and return to high tide roosts. Channing and Craig (1954) censused a 100-acre plot at high water and low water and obtained the average number of birds using the plot at these times. Pugh (1963) censused a 2-mi strip of tidal mud flat within two hours to either side of low tide to obtain the average number of birds per mile. Cogswell (1966) and Cogswell and Lawrence (1965) censused a mud flat plot at various times of the tidal cycle and obtained the average number of birds using the plot under various schedules of tidal fluctuation. Recher (1966) reported that an accurate representation of species composition occurred on the falling phase of a minus or near minus tide after 30 to 60% of the tidal mud flat was exposed.

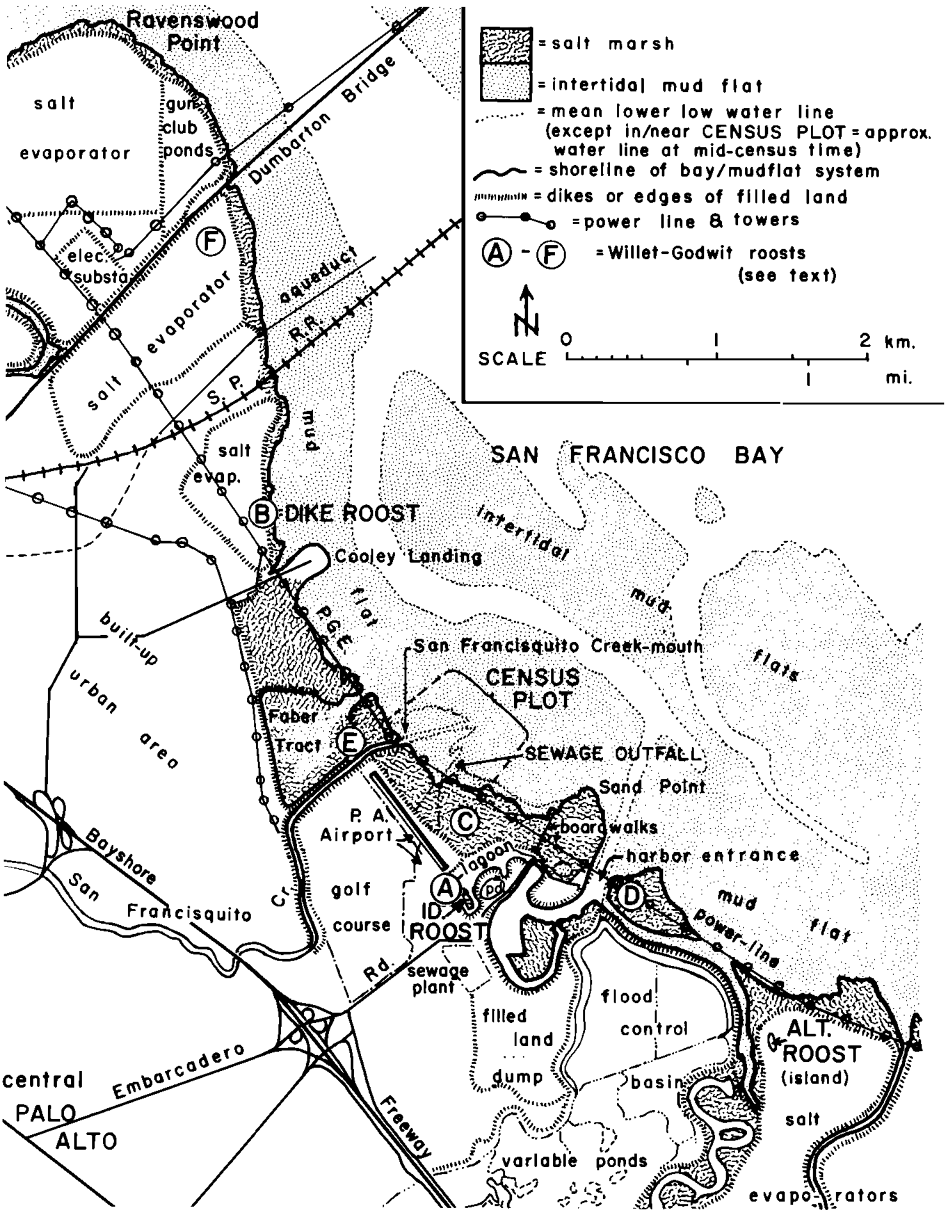

FIGURE 1. Study area on San Francisco Bay.

Using a census plot at the mouth of San Francisquito Creek (Fig. 1), an attempt was made to census Willets and Godwits when one-third of the mud flat was exposed on the ebb phase of a minus or near minus tide (approximately 4 h 45 min after a high tide of about seven feet or more at Palo Alto). At this time there were about 25 ha of exposed mud in the plot. This method usually resulted in the maximum number of Willets and Marbled Godwits within a distance at which they could be identified. However, there are times when falling tides occur only during hours of darkness, and during some periods of the year no minus low tides occur during daylight hours. These factors resulted in time gaps and sporadic collection of census data at certain times of the year. Obvious landmarks such as permanent wood structures on the mud flat were used to determine tide level during a census. The census plot was scanned with a spotting scope and each Willet and Marbled Godwit seen was recorded. The duration of a census varied during the year from a few minutes to about 30 min.

Counts or careful estimates were made at high tide roosts where birds were usually closely packed. Presence or absence of birds at these high tide roosts, or in any habitat in the study area, was noted.

The majority of field time was devoted to observations of tagged Willets and Marbled Godwits. Ninety-eight birds were captured on 19 February 1973, with a cannon-net at roost A (Fig. 1) using techniques similar to those described by Gerstenberg (1972). The birds were banded, individually marked with patagial tags bearing numbers, and released within six hours. The tags are similar to those used on gulls by Diem (1967), Diem and Condon (1967), and Cogswell (1970, 1974).

Searching for and reading numbers on tagged birds was done mainly in the study area although high tide roosts and mud flats as far away as the Hayward shores, 18.5 km to the north, and the Alviso shores 8 km to the south, were checked occasionally. High tide roosts known to be used by tagged birds were frequently checked and an attempt was made to determine tag numbers with a spotting scope. The tidal mud flat including the census plot was also searched for tagged birds. Tag number, date, time, habitat, and behavior of any marked individual identified were recorded. An individual was only recorded more than once on a given day if it was observed more than about 300 m away from the initial location, or more than one hour after the initial sighting.

Tags were more noticeable on active birds on the mud flat as their movements tended to uncover the numbers on the tags, which were sometimes partially covered by the scapular feathers. In good light on a cool, calm day tags could be seen on birds as far away as 1500 m and a clearly visible number could be read at 800 m. Sleeping or inactive birds were often able to conceal the main part of a tag, thus making numbers difficult to discern. Circulars requesting specific information on observations of tagged birds were posted at various locations in the San Francisco Bay area and mailed to museums, schools, and wildlife management agencies in western North America.

RESULTS AND DISCUSSION

HABITAT USE

Within the study area Willets and Marbled Godwits were found to use two high tide roosts (A and B, Fig. 1) consistently, although occasionally one alternate roost (C) was used. Roost A, the usual and most important roost in the Palo Alto area, was on an island in an enclosed lagoon. The island was separated from the mainland by about 5 m at the narrowest channel. Willets, Marbled Godwits, Dowitchers (*Limnodromus* spp.) and to a lesser extent smaller shorebirds would roost on salt grass, pickleweed and areas of bare mud within the vegetation. Difficulty was sometimes encountered in distinguishing between Willets and Marbled Godwits which packed together tightly among the vegetation. The combined numbers of Willets and Marbled Godwits which utilized this roost ranged from 1700 birds in January 1973 to none during May and June 1974. This roost served as the capture site and the site of many subsequent tag sightings.

Occasionally this roost was abandoned in favor of an alternate roost (C) in the Palo Alto salt marsh. This switch could sometimes be explained by a disturbance at the island roost or by an unusually high tide which would force the birds from the island to the higher portions of the salt marsh. On a few occasions, neither the island roost nor the salt marsh roost was utilized. At such times numbers of birds were found in other high areas of the salt marsh.

The other important high tide roost in the area is located on a salt pond dike, 300 m north of Cooley Landing (B, Fig. 1). The dike, composed of dried dredging spoils, borders on San Francisco Bay; thus the birds at this roost were only a few feet from the mud flat as the tide ebbed. The birds favored the top or the side of the dike away from the bay as this was normally the leeward side. The roost was only censused on occasion as it played a minor role in the behavior of tagged birds. It was first observed on 26 September 1973 when it was used by 340 Willets and 410 Marbled Godwits, and was subsequently censused four times (28 September 1973, 289 Willets and 362 Marbled Godwits; 12 October 1973, 110 Willets and 58 Marbled Godwits; 21 March 1973, 102 Willets and 133 Marbled Godwits).

The salt pond just south of the Dumbarton Bridge (F) was at times used by large numbers of shorebirds. These were usually Willets, Marbled Godwits, and Avocets (*Recurvirostra americana*) as smaller species could not stand in the relatively deep water. The use of this pond was noted from August 1973, through November 1973, and combined numbers of Willets and Marbled Godwits were estimated on 24 August (1600), 12 October (300), and 18 November (3100). Movements between the mud flats in the vicinity of Cooley Landing and this pond were observed on 24 August 1973 when an estimated 1000 birds were observed to make this flight. Use of this salt pond may explain the reduced numbers observed at the island roost from August through December 1973.

Gerstenberg (1972) found that Willets fed in the salt marsh as the tide began to recede, as they did on the present study area. Loose flocks as large as 35 birds were seen foraging in many parts of the marsh prior to and after feeding on the mud flat. On only one occasion, 11 April 1974, were Marbled Godwits observed foraging in a salt marsh, when about ten birds were seen at the mouth of San Francisquito Creek, while other shorebirds fed on the exposed mud flat. The mouth of San Francisquito Creek served as the major feeding grounds for shorebirds in the study area.

MOVEMENTS IN RELATION TO TIDE CYCLES AND WEATHER

During an ebb tide at Palo Alto, large shorebirds would normally arrive at the mud flat shortly after mud was exposed. Initially, birds would begin to leave the high tide roosts for the mud flats individually. Later, usually within 15 min, small groups would depart and within one-half hour the majority of the birds would depart. Marbled Godwits were observed to fly from the island roost (A), from the alternate roost in the salt marsh (C), and from the Cooley Landing dike roost (B) to the Palo Alto mud flats, mainly the mouth of San Francisquito Creek (Fig. 1). Mixed flocks of Willets and Marbled Godwits were often observed during these ebb tide flights; however, Willets were seldom seen to come from the Cooley Landing dike roost to the Palo Alto mud flats, and Marbled Godwits tended to be more gregarious. Behaviors exhibited during these flights were similar to those observed by Luther (1968). Marbled Godwits coming to the Palo Alto mud flats from the Cooley Landing dike roost consistently flew a wide path over the water around Cooley Landing rather than taking the shorter path across land. This behavioral trait was noted for many shorebirds when moving to and from tideflat feeding areas on the San Francisco Bay.

Marbled Godwits tended to arrive at the mud flat prior to Willets, and assembled at the water's edge about 200 m southeast of the Palo Alto sewage outfall where mud is exposed early. From this point, the Marbled Godwits would follow the receding water but also move northwest to the mouth of the sewage outfall while being joined by other Marbled Godwits. This movement was interpreted as an attempt to feed into the wind which usually blows out of the northwest and to reach the sewage outfall which seemed to concentrate shorebirds. Main arrival occurred within 30 min and both Willets and Godwits would forage while moving north to the creek mouth. At this point the birds would forage along the creek mouth or over delta formed by the creek.

At times, tides with small (short) tidal exchanges would occur. These would result in Willets and Marbled Godwits packing together at the mouth of the sewage outfall where the first mud is exposed in the Palo Alto area. On 12 April 1973, 75 Marbled Godwits and 55 Willets were observed waiting there as the ebbing tide had not yet exposed mud following a previously rather high low tide of +2.2 ft. Such tides result in only small areas of mud being exposed and in a shortened feeding period. Luther (1968) has shown that arrival time is dependent on the length of time the mud was exposed during the previous low tide. In addition, strong winds can pile up water and delay the exposure of the mud flat by approximately one-half hour.

During or following periods of rain, both roosts A and C (Fig. 1) were often abandoned in favor of flooded fields and a golf course. On 9 January 1973, 130 Marbled Godwits were observed feeding on the lawn of the Palo Alto golf course following a period of rain. Gerstenberg (1972) observed the same behavior and mentioned that it may have been caused by siltation on the mud flat making regular food items temporarily unavailable, or flooding of uplands making probing easier and causing earthworms and other macro-organisms to rise to the soil surface. On several occasions during very high tides which flooded the roosts, or after rain, or following previously high low tides, few birds could be found in the study area and they were suspected of roosting or foraging in some flooded area such as the Palo Alto flood basin.

CENSUS DATA

Census data for the Willet from April 1973 to May 1974 are shown in Figure 2. Reduced numbers due to spring migration are evident in April with a low in the population during May and a return during June. The peak population of 867 birds was recorded on 12 October 1973, with a subsequent decline during the winter and spring to about 300. This was followed by a rapid decline during April 1974 to only five birds on 3 May 1974. Storer (1951) found the migration pattern of the Willet at Alameda-Oakland to be puzzling as a fall peak was found in late September and early October, but the wintering population was considerably lower until March when the species became scarce. Recher (1963) recorded a fall peak at Palo Alto in late October followed by a rapid decline, and spring peak in mid-March with a rapid decline in April. Jehl and Craig (1971) recorded peak numbers at San Diego in August with large numbers also present in February, March and April. Gerstenberg (1972) found that peak fall flights at Humboldt Bay occured in mid-July and late August and spring movement occurred from late March to mid-April. Jurek(1974) tends to confirm these observations. Considering these data with those from the present study, a shift in peak numbers can be observed from northern to southern California, with fall peaks in north in July and August, peaks in central California in September and October, peaks in southern California (disregarding the August peak) from October through November. Large numbers of birds appear to remain in southern California through the winter into the spring. Thus, there appears to be a movement of Willets from

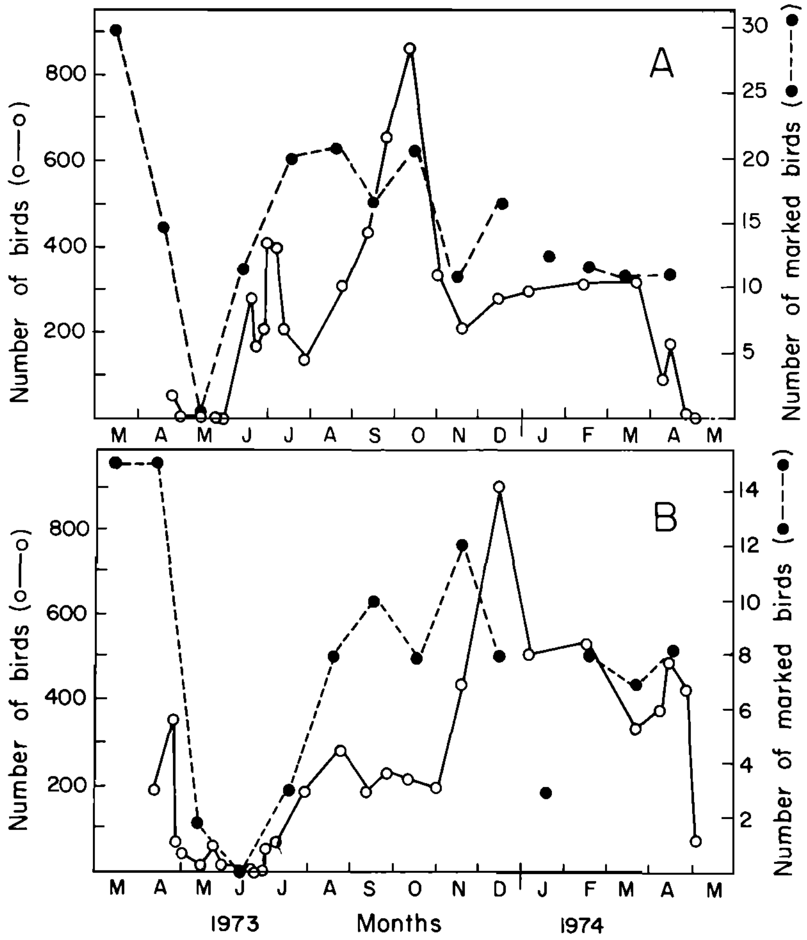

FIGURE 2. Number of birds observed on census plot and number of tagged birds present in the study area March 1973 to May 1974. A, Willet; B, Marbled Godwit.

northern California to southern California through the fall and winter, resulting in the observed fall peak at Palo Alto on 12 October 1973 (Fig. 2), with a subsequent decline in November. No consistent peaks are shown during spring migration but numbers decline rapidly in all parts of the state in April.

The apparent drop in Willet numbers during July and August 1973 (Fig. 2A) illustrates the need to plan census dates carefully as the data obtained in those months are thought to be inaccurate. On 13 July 1973, shorebirds were censused during a very "high" low tide of +3.2 ft following a previous "low" low tide of −0.4 ft. This resulted in a low count, as many Willets did not come to the mud flat to feed. During this low tide many Willets were seen in the salt marsh but an accurate count was not made. A similar situation occurred on 29 August 1973, when the period of censusing fell during a relatively "high" low tide of +3.0 ft following a relatively "low" low tide of −0.7 ft.

Census data for Marbled Godwits (Fig. 2B) show numbers dropping off rapidly during April and reaching a low in June. The numbers of birds increased during

July to about 200 and remained fairly constant until further increases during November led to a peak of 902 birds on 14 December 1973. Numbers then declined rapidly to about 350 to 550 birds, remaining thus until there was a sudden decrease due to spring migration (late April in 1973, early May in 1974).

Storer (1951) observed peak fall flights of Marbled Godwits in September and a peak spring flight in April. Two large peaks reported by Storer (1951) in January and February were doubted by Luther (1968) who indicated that the fluctuations may have been due to the presence of birds in alternate feeding areas not being censused by the investigator. Recher (1966) had incomplete data for the fall migration at Palo Alto but showed spring peaks in April and May. Luther (1968) showed a fall peak at Hayward in December and a spring peak in April. Jehl and Craig (1971) observed high numbers at San Diego in January followed by a slight decline and a peak in April. Gerstenberg (1972) observed fall peaks at Humboldt Bay from August through October with a decline in December, and spring peaks from April to May. Jurek (1974) shows fall peaks in central and southern California from October through January. Excepting Storer's (1951) data, Marbled Godwits tend to show a southward movement in peak numbers through California during the fall and winter. Luther (1968) and the present data show peaks in December, and Jehl and Craig (1971), to the south, show fairly high numbers from January through April. All of the forementioned investigators showed large peaks of Marbled Godwit numbers in April and May while the present study shows only a minor peak in April. During the present study four censuses were made between 21 March 1974 and 26 April 1974; however, one 18-day gap and one 9-day gap may have resulted in the missing of the major peak of the spring migration. Jehl (1968) found that some shorebird movements may be missed if censuses are taken at intervals less than a week.

Luther (1968) found a major departure of Marbled Godwits in late April and the present study similarly demonstrates a rapid decline in their numbers in late April and early May. Gerstenberg (1972), however, mentions a group of 400 Marbled Godwits that was seen summering until late June in the Humboldt Bay area of California, the northernmost coastal bay where they are common. Although it is not unusual to see small numbers of summering Marbled Godwits in the San Francisco Bay area, Gerstenberg's large numbers may, as he mentioned, support Loftin's (1962) findings that some shorebirds migrate north of their wintering range but do not breed and later move south, previous to or with breeders.

TRAPPING AND TAGGING

Of the shorebirds captured, 49 were Willets and 45 were Marbled Godwits. There were no mortalities resulting from the capture. Three distressed birds were released untagged. All others were tagged. One bird was found dead and one loose tag was recovered shortly after tagging was conducted. After these known losses, a maximum of 46 Willets and 43 Marbled Godwits presumably remained tagged. Of these, 20 Marbled Godwits (47%) and 17 Willets (37%) presumably left the area immediately as they were not seen again prior to the spring migration. These seemingly premature departures may have been caused by the trapping experience, although some of these birds returned the following fall. These data and the following discussion are based on 567 observations of 40 Willets and 30 Marbled Godwits.

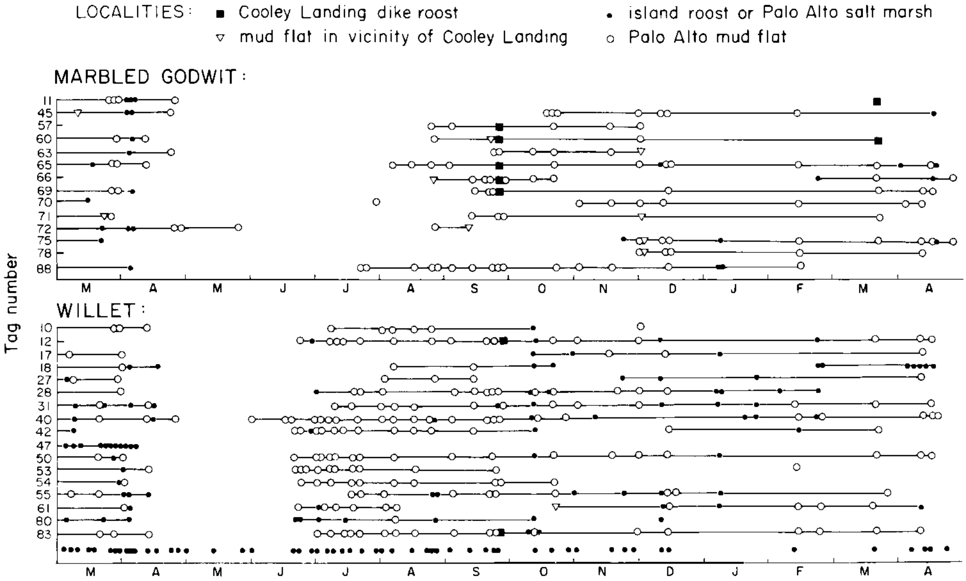

FIGURE 3. Dates and locations of observations of tagged Marbled Godwits and Willets in the study area March 1973 through April 1974. Dots just above the lower horizontal axis indicate dates of searches for tags. Lines connecting plotted points indicate periods of presumed minimal continuous residence in the study area. Willets plotted are those seen nine or more times during the study; Marbled Godwits are those seen seven or more times.

Observation of tagged birds.—Table 1 shows the number of tag observations of Willets and Marbled Godwits made in each section of the study area and the percentages of the total that these observations represent. It is apparent from the data that most tagged birds roosted on the island (A) or adjacent salt marsh (C) and fed at the mouth of the San Francisquito Creek. Figure 3 shows the dates and locations of all observations of tagged Willets seen nine or more times during the study (17 birds), and of tagged Marbled Godwits seen seven or more times (14 birds). Observation of birds not included in these figures were infrequent but otherwise similar to those considered here unless stated otherwise in the following discussion. It can be seen from these data that tagged birds observed repeatedly demonstrated a habitual use of certain roosts and areas on the mud flat. Willet no. 40, for example (Fig. 3), was observed 34 times during 14 months only on the Palo Alto mud flat, in the Palo Alto marsh, and on the island roost.

Marbled Godwits exhibited the same habitual use of certain roosts and feeding areas, but they tended to disperse more than Willets and were found to a greater extent on mud flats north of the mouth of San Francisquito Creek and on the Cooley Landing dike roost. Seven observations of six individual Marbled Godwits were made at this roost (tag numbers 11, 57, 60 (twice), 65, 66, 69; Fig. 3). Two tagged Marbled Godwits (65, 66) returned to the island roost after being seen at the dike roost and one Marbled Godwit (60) was thought to have joined the dike roost permanently (Fig. 3). Willets engaged in this exchange less frequently as only three observations of three individuals (12, 38, 83) were made in the Cooley Landing area and two of these birds (12, 83) were later seen on the island roost

TABLE 1

OBSERVATIONS OF TAGGED BIRDS MADE IN SECTIONS OF THE STUDY AREA

Habitat	Marbled Godwit		Willet	
	N	%	N	%
Roost A	27	14.7	37	9.7
Roost B	7	3.8	3	0.8
Roost C	5	2.7	78	20.4
Mud flat—sewage outfall to Faber Tract	97	52.7	157	40.9
Mud flat—sewage outfall to harbor entrance	24	13.0	95	24.8
Mud flat—Faber Tract to Cooley Landing	7	3.8	2	0.5
Mud flat—Cooley Landing to RR bridge	11	6.0	1	0.3

and in the Palo Alto salt marsh (Fig. 3), Willet no. 38 was not included in Figure 3 since it was observed only six times during the course of the study.

The above observations, however, are exceptions to the usual behavior of most tagged birds already summarized. The latter provide a good indication of the restricted nature of the home range of most individuals of these species on their wintering ground near Palo Alto. The distance from the island roost to the feeding grounds is about 1000 m, a distance much less than the feeding flights of up to 6100 m described by Luther (1968).

It would appear from Table 1 that Willets utilize the salt marsh much more than Marbled Godwits. This is the case but not to the degree indicated by the data. These figures do not provide an absolute measure of habitat use, since the observer's ability to find tags in various habitats varies considerably. Marbled Godwits in the salt marsh and on the island roost packed together tightly, usually slept, and moved little, thus making tag reading difficult. This behavior resulted in a bias in numbers of tag sightings between high tide roosts and on the mud flat (Table 1). In contrast, Willets were often active in the salt marsh and displayed their tags readily. Such behavioral differences were minimized on the mud flat when tags of both species could be read with equal case.

Movements of tagged birds of more than 300 m while feeding on the mud flat were very unusal. Two such movements were observed on 30 November 1973, when tagged Marbled Godwits (numbers 75, 78) moved from the creek mouth to north of Cooley Landing during the same low tide, a distance of 1700 m.

Gerstenberg (1972) describes the frequent use of the salt marsh by Willets but no investigator of salt marsh populations has mentioned the total avoidance of tidal mud flats by some Willets. From 4 March 1973 to 5 April 1973, one tagged Willet was observed 11 times in a small area of the Palo Alto salt marsh during all phases of the tidal cycle and never elsewhere. Another tagged Willet was observed to behave similarly and was observed ten times in a small section of salt marsh from March 1973 to December 1973. It is believed that these birds were not injured or abnormal as the latter bird was eventually seen on the mud flat one-half mile away and other untagged Willets were sometimes seen in the vicinity of these tagged birds. Recher (1963) has described instances of territoriality in shorebirds especially where vegetation is broken up by puddles and mud, as in the section of salt marsh where the tagged Willets foraged, but no instances of aggressive interaction were observed. The possibility remains, however, that the birds were occupying feeding territories.

TABLE 2

Maximum Interval of Absence from Study Area for Tagged Birds during Summer 1973

Willet		Marbled Godwit	
Tag no.	No. of days	Tag no.	No. of days
10	85	45	181
18	110	60	135
24	99	63	154
27	124	65	115
28	89	69	160
31	85	70	133
42	105	71	150
50	84	72	92
53	70	88	115
54	86		
55	95		
61	79		
80	79		
83	78		
Means:	91 days		137 days

Note: Willet no. 40 omitted because bird may have summered. Willet no. 17 and Marbled Godwit no. 75 omitted because it is likely that they were overlooked in early fall 1973.

Two reports of tagged godwits outside the study area were received. One was observed on 6 May 1973, in southwestern Idaho at the junction of the Snake and Boise rivers. The bird was the only one of its species feeding in a field with Willets and American Avocets. The bird flew off when approached and was not seen again. According to the observer, Marbled Godwits are seldom seen in that area. The bird had no prior resighting record in Palo Alto and has never been seen again. It is suspected that the tag may have interfered with flight during migration and caused the bird to separate from its flock. Another godwit was observed on 6 May 1973, in southwestern Alberta, near the town of Indus, 15 mi southeast of Calgary. The bird was in the company of other godwits, which breed in the immediate vicinity. This is the first instance of a banded Marbled Godwit from the wintering grounds being found on the breeding grounds. The bird was able to fly and appeared normal. It was seen three times on the Palo Alto mud flat prior to its departure (last observation 24 April 1973), but not again after the Alberta sighting. The sightings of tagged Marbled Godwits in southwestern Idaho and southwestern Alberta indicate the possibility of a flight path from the wintering grounds on a north-northeast heading to breeding sites in southern Alberta.

Another tagged Marbled Godwit (number 57) was seen for the first time on the Hayward shore of San Francisco Bay 18.5 km north of the study area on 3 August 1973. It was subsequently seen at Palo Alto on 24 August 1973, and on five other occasions through November 1973.

Two Willets were seen outside the study area. The first (number 28) was observed on 26 June 1973, at Bolinas Lagoon 45 mi north-northwest of the study area. This bird was previously seen 19 times beginning 29 June 1973 (three days after it was at Bolinas), and extending to 25 February 1974. The second was found dead on 6 June 1976, near Beckwourth, Plumas County, California, at an elevation of about 1500 m where this species breeds in small numbers. This bird had only been seen once before at Palo Alto, on 25 August 1973.

Fifteen Marbled Godwits, 35% of those originally tagged, and 30 Willets, 65% of those originally tagged, returned to the Palo Alto area after presumably migrating. In view of the faithfulness for the wintering grounds exhibited by the tagged birds, it is thought that most of those that failed to return had probably died.

The interval of absence from the study area during the breeding season was calculated for those tagged Willets and Marbled Godwits for which repeated observations offered evidence of departure and arrival. These data are shown in Table 2. For Marbled Godwits the mean interval of absence was 137 days (N = 9). For Willets it was 91 days (N = 14). The minimum observed interval of absence was 70 days for a Willet, with the exception of number 40 which may have been a nonbreeder. This interval would suffice for a bird that migrated directly to the breeding grounds to then nest and raise young.

Recher (1966), Swinebroad (1964), and Post and Browne (1976) have discussed the length of time that a shorebird spends in an area during migration. Recher (1966) mentions occasional distinctive individuals which were observed over a 1-mo period. He found that those individuals were remarkably constant as to feeding and loafing sites they frequented. He often observed equally distinctive birds that were observed once and then left the area (no dates or species were mentioned). Recher (1966) concluded by examining his own census data and those of Storer (1951) that a shorebird's presence is temporary in any one area on the wintering grounds. As previously mentioned, his data showed population peaks that were interpreted as successive groups of birds moving into and out of an area.

Recher (1966) believed that the influx of migrants into an area would lead to dispersal within and migration out of the area by the former "residents" which would be behaving as a group, due to their similar physiological and psychological levels (thus, the successive waves). This, he believed, would minimize interspecific interactions that might result in competitive exclusion. Until then, the few available returns from banded birds had not clarified the problem. In the Humboldt Bay area, for example, Gerstenberg (1972) recaptured five Marbled Godwits in the fall, 56 days after banding, and one Willet was found dead 75 days after banding.

Our results, however, show that many individual tagged birds were present in the study area for eight to nine months of the year. Nevertheless, Recher's conclusions may apply to some degree. Figure 2 compares the numbers of individual tagged birds observed per month to the total population on the census plot. A decrease in the number of tagged birds in the study area was noted after the winter peaks. However, about two-thirds of the observed maximum number of tagged birds seen after fall return were present after the winter peak. It appears, then, that about one-third of the tagged birds that migrated back may have left the study area for more southerly areas after the winter peaks, while the majority of the tagged birds remained in the study area.

The winter peaks in numbers of Willets (October) and Marbled Godwits (December) on the census plot can be examined in relation to the observed migratory departure and arrival dates for tagged birds (Table 3). The mean arrival dates for tagged birds of both species precedes the winter population peaks by two to three months; and as shown above, the tagged birds were for the most part independent

TABLE 3

Migration Dates for Tagged Birds

	Departure			Arrival			Population peak
	N	Mean date	Range	N	Mean date	Range	
Willet	18	6 April	±9 days	27	1 August	±47 days	12 Oct
Marbled Godwit	12	21 April	±13 days	14	13 Sept	±43 days	14 Dec

of the winter peaks and subsequent declines. Bent (1927, 1929) reported that adult Willets and Marbled Godwits leave the breeding grounds before juveniles and this was confirmed for Marbled Godwits by Gerstenberg (1972) when only six birds out of 256 trapped between August 15 and October 11 were in juvenile plumage. These findings may explain the early migration arrival dates of the tagged adults birds and their dependence (for the most part) from a subsequent influx of juveniles comprising the winter peaks observed in October (Willets), and December (Marbled Godwits).

Significance of observations of tagged birds.—Individually marked Marbled Godwits and Willets have provided the first opportunity to examine the habitat preferences and local and migratory movements of individual birds within a wintering population. Marked birds demonstrated a habitual use of roosts in the Palo Alto salt marsh and mud flats at the mouth of San Francisquito Creek. These observations and the few exceptions observed demonstrated the restricted nature of the home range of the tagged individuals.

A comparison of the migration departure and arrival schedules of marked and unmarked birds was revealing. Tagged birds departed along with unmarked birds but arrived considerably earlier than the winter population peaks which probably represent a southward movement of juveniles.

Most of the tagged birds observed were present in the study area for about eight to nine months of the year, and were for the most part independent of winter population peaks. These findings demonstrate that Recher's (1966) general conclusion that a shorebird's presence is temporary in any one area on the wintering grounds is false. Without marked birds, it cannot be assumed that population peaks or waves of the birds moving into and out of an area reflect a turnover in local populations.

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SEMIPALMATED SANDPIPER MIGRATION IN NORTH AMERICA

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ABSTRACT—Morphometric studies of adult Semipalmated Sandpipers from museum collections and banding operations show that spring and autumn routes in North America are different, and that the routes used are not the same for birds from different parts of the breeding range. In spring, breeders from Alaska and central Canadian arctic zones follow a central North American route, whereas eastern Canadian birds follow an Atlantic route. In autumn, Alaskan breeders retrace the spring route, with some possibly using more eastern corridors; central Canadian birds use an Atlantic route, with most apparently travelling far east of their spring route. Eastern Canadian breeders continue to use an Atlantic route in autumn, possibly somewhat east of their spring route.

Although the migratory movements of shorebirds across America have long been known in general terms, there is a remarkable scarcity of detailed studies of the movements of individual species. Detailed knowledge of the migration patterns and strategies of populations from different parts of the arctic is a prerequisite for the identification of sites that are of critical importance to the well-being of shorebird populations. We provide the first such account for one of the most numerous of North American shorebirds.

The Semipalmated Sandpiper (*Calidris pusilla*) breeds in a broad zone from the Alaskan Arctic coast across Canada to northern Quebec, central Baffin Island and northern Labrador, apparently in three disjunct populations (Manning, Höhn & MacPherson 1956, A.O.U. 1957, Palmer 1967). Birds from eastern parts of the breeding range have longer bills than those from western areas (Manning et al. 1956). The species is therefore well suited to comparative studies of migration strategies using morphometric studies made at stopover and wintering areas.

It has been believed for some time that the spring and autumn migration routes of Semipalmated Sandpipers are somewhat different (Loftin 1962, McNeil and Burton 1973, 1977). In this report we review and assess information on Semipalmated Sandpiper migration provided by morphometric data and indices of migrant abundance which we and others have collected. The data confirm that many Semipalmated Sandpipers use different routes for northward and southward migration. An 'elliptical' migration route involving a northward spring migration through central areas of the U.S. and Canada followed by a southward autumn migration via coastal areas along the eastern seaboard is used by many birds, particularly those from central parts of the breeding range. Birds from the extreme eastern and western parts of the range tend to migrate along the eastern and western edges of these routes, respectively, in both directions.

METHODS

In Massachusetts our studies were carried out principally at Plymouth Beach (41°55′N, 70°37′W), a 4.5 km sandy peninsula that extends into Plymouth Bay near the base of Cape Cod (Fig. 1). As many as 5500 Semipalmated Sandpipers roost on the beach during high tides in late July and early August, and the species outnumbers all others combined during most of the autumn migration period. From 1972 through 1976, shorebirds were counted while roosting at Plymouth Beach at least weekly from 1 July through 31 October, and almost daily from mid-July through September. Censuses in

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spring were less systematic, sometimes made twice weekly, but normally only once every ten days. During all censuses, individually color-marked birds and ratios of banded to unbanded birds were recorded.

Mist nets were used to capture Semipalmated Sandpipers near the outer end of Plymouth Beach. Twelve-meter long nets were erected soon after high tide, on aluminum poles sunk into sand under about 15 cm of water. Trapping was usually carried out at night, the nets being moved about every half hour as the tide fell.

Birds captured at Plymouth were held in a large, well-ventilated holding box and returned to the banding laboratory about 7 km away at the Manomet Bird Observatory for processing. Information recorded included exposed culmen length (feathers to tip of bill) to the nearest 0.1 mm, weight on a triple-beam balance to the nearest 0.1 gm, unflattened (natural) wing length to the nearest mm, and a subjective assessment of the amount of subcutaneous fat on a scale of 6. Samples of each catch were examined for molt. Banded birds were usually released at Plymouth Beach, but sometimes at Manomet: the latter were seen subsequently at Plymouth Beach as often as those that were returned to the Beach.

Banding studies in James Bay were carried out in 1975, 1976 and 1977 at North Point (51°29′N, 80°27′W), on the southwest coast of James Bay, approximately 27 km northeast of Moosonee, Ontario (Fig. 1). The coast is very flat, with extensive marshes. Mist-netting was the principal trapping technique, although cannon nets were used when appropriate conditions occurred. From 70–150 mist nets were erected in lines of up to 17 nets over a 2 km stretch of coast at the junction of the saltmarsh and tidal flats, to intercept flight lines of birds moving to high tide roosts. Nets were checked continuously during suitable weather on a 24-hour basis using all terrain tricycles. Birds were returned 1 km to the camp for processing, which included measurement of wing (maximum length stretched and flattened to the nearest mm), bill (exposed culmen to 0.1 mm), weight (Pesola spring balance to 0.5 g), examination for molt, and color dyeing and color-banding. They were returned to the coastal marsh for release near the place of capture.

Bill (exposed culmen) and wing (flattened and/or unflattened) measurements were also made on a large number of museum specimens. All birds showing damaged or molting distal primaries were excluded. To enable comparison of wing lengths measured by the two authors to be made, each measured a series of either the same (live) or directly comparable (specimens) birds. The difference (RIGM = BAH + 2 mm for museum specimens, RIGM = BAH + 6.8 mm for live birds) has been allowed for in discussing comparisons of wing measurements and in calculating bill/wing ratios, as noted in Tables 2 and 3. No difference was found between bill measurements made by the two authors. Unless noted, measurements of live or fresh specimens were not compared with those of dried museum specimens owing to problems caused by shrinkage (e.g. Vepsalainen 1968, Prater et al. 1977). Last, unless noted measurements from juveniles are excluded from analyses owing to problems of comparability including, for example, the facts (i) that museum specimens from breeding areas include juveniles with incompletely grown bills, and (ii) that juveniles caught at stopover areas tend to have shorter wings than adults of comparable bill length.

The coefficient of variation (CV) has been used to compare the variability of bill measurements between different seasons and places where samples have different means, as well as to compare the variability between measurements of museum specimens and live birds, since the CV is independent of the units of measurement (Simpson, Roe and Lewontin 1960). Statistical differences between CV's were tested using the *t*-test described by Dow (1976). Analysis of variance was used to test the statistical significance of differences between sets of measurements, and frequency data were compared using a chi-square test (Sokal and Rohlf 1969).

RESULTS

REGIONAL STATUS DURING MIGRATION

Spring migration

Palmer (1967) noted that most of the spring migration of Semipalmated Sandpipers in the coterminous United States occurs in the middle two weeks of May. While this is generally true, regional variations seem to exist. In Louisiana (Lowery 1974) and northern Florida (Loftin 1960, 1962), Semipalmated Sandpipers are most common in late April/early May, but have gone by late May/early June

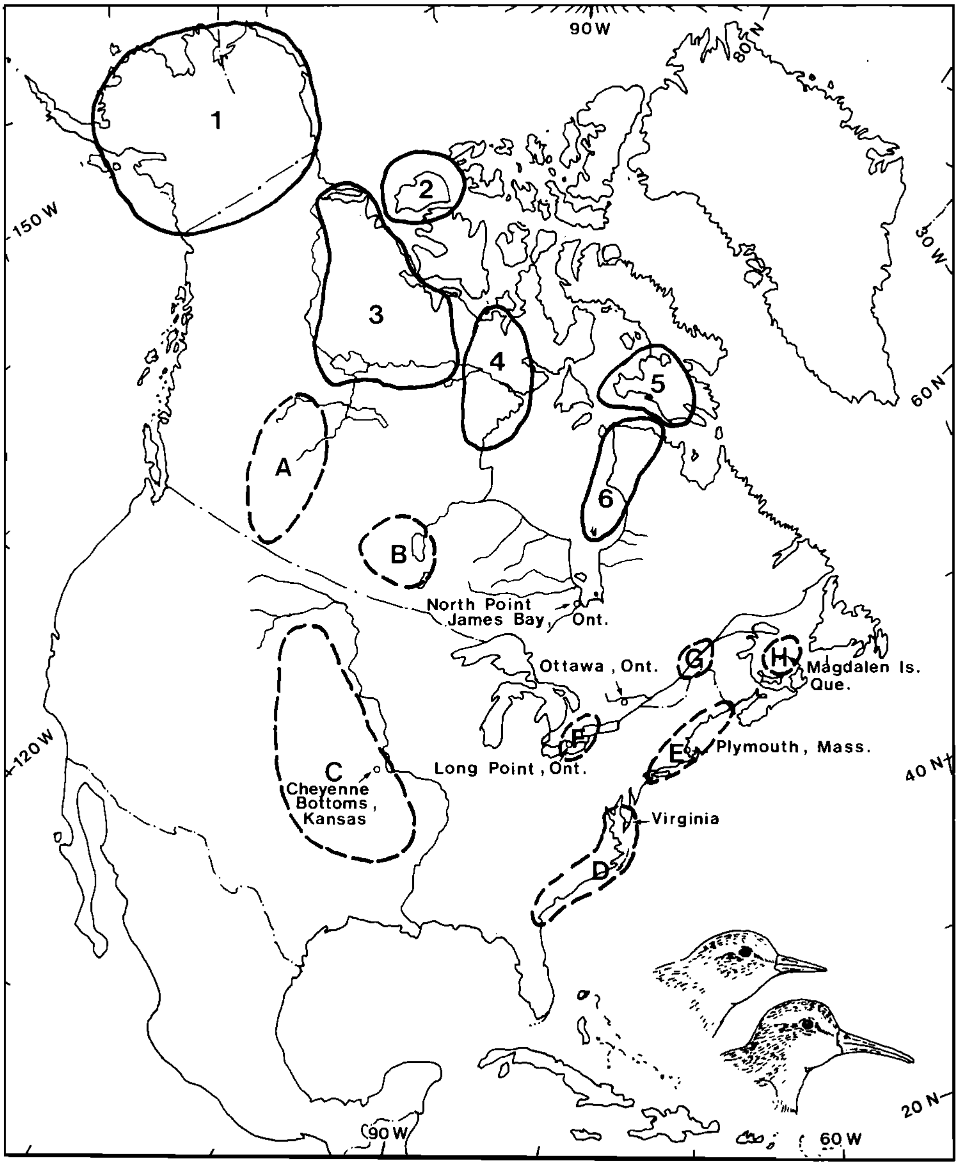

FIGURE 1. North America, showing locations of banding studies referred to in the text and in Table 4, and areas from which measurements of museum specimens were collected for morphometric studies (Tables 2 and 3).

Breeding areas (solid lines, numbers, see Table 2): 1. Alaska, 2. Banks Island, N.W.T., 3. Mackenzie district, N.W.T., 4. Keewatin district, N.W.T., 5. West Baffin Island, N.W.T., 6. Belcher Islands, N.W.T., and East Hudson Bay, Quebec.

Migration areas (broken lines, letters, see Table 3): A. Alberta, B. Saskatchewan/Manitoba, C. Central U.S., areas between the Mississippi River and the Rocky Mountains, D. Maryland to Georgia, E. New York to Maine, F. Southern Ontario, areas between Toronto and Long Point, G. Kamouraska, St. Lawrence River, Quebec, H. Magdalen Islands, Gulf of St. Lawrence, Quebec.

Heads of the short-billed and long-billed forms of the Semipalmated Sandpiper from western and eastern arctic breeding areas, respectively, are illustrated.

(Loftin 1962). In Oklahoma (Oring and Davis 1966), Kentucky (Mengel 1965), Ohio (Trautman 1940) and central Kansas (Parmelee et al. 1969), highest counts also occur between late April and late May. In the Drumheller area of Alberta, the main passage occurs in the latter half of May (Kondla et al. 1973), as it does in northern Saskatchewan (Houston and Street 1959).

On the east coast the seasonal pattern is somewhat different, especially in the northeast where peak counts are found in late May or early June. At Daytona Beach, Florida, Longstreet (1934) did not find Semipalmated Sandpipers in April, they were abundant in May, and they were virtually absent in June. In Maryland, the species is most common in May (Stewart and Robbins 1958), but moderate numbers also occur in the first third of June. In New Jersey, peak spring counts are in mid-May (Urner and Storer 1949), but high numbers are still found in early June. In New York, spring maxima occur in the latter half of May and early June (Bull, 1974).

In Massachusetts the peak of spring migration is usually between 25 May and 7 June (Bailey 1955). Highest numbers occur in eastern parts of the state, e.g., on Cape Cod where estimates of as many as 25,000 have been made on 30 May (Hill 1965) and 35,000 on 1 June 1957 (Bailey 1968), about double the maximum numbers found in the same area during autumn migration. At Plymouth, small flocks normally appear in mid-May, but peak numbers (about 1500 birds) do not occur until late May or, more often, in early June. Counts of as many as 5500 birds are made at Plymouth in autumn migration.

At points north and east of Massachusetts, adult Semipalmated Sandpipers are much less common in spring than autumn. In Maine they are "common" in spring from the middle of May to the end of the first week in June, and "abundant" in autumn (Palmer 1949). At Mary's Point, New Brunswick, on the upper Bay of Fundy, the species is much more numerous in autumn than spring, the northward passage occurring during the latter part of May and early June (D. S. Christie, Maritimes Shorebird Survey observations, pers. comm.). In Nova Scotia, Tufts (1973) describes the Semipalmated Sandpiper as rare in spring, but common in autumn. In Newfoundland they are absent in spring, yet regular in autumn (Godfrey 1966).

In the Great Lakes area, passage dates of Semipalmated Sandpipers are generally in late May. At Kingston, Ontario, arrival dates average 22 May with most birds gone by 30 May (Quilliam 1973), and at Point Pelee on Lake Erie, the passage occurs at the end of May (Stirrett 1973). In the Cleveland Region, peak passage dates are in the last ten days of May (Newman 1969). At Ottawa, Ontario, and Montreal, Quebec, the peak passage occurs at the very end of May and early June (P. Hamel, pers. comm., S. Holohan, pers. comm.).

Autumn migration

In Newfoundland there are no July records of Semipalmated Sandpipers and highest counts, most from the southwestern part of the province, do not occur until late August or the first half of September (Peters and Burleigh 1951). The main passage of migrants in Labrador does not occur until about the third week in August (Austin 1932). This is long after maximum numbers of adults occur at James Bay and Plymouth, but is when highest numbers of juveniles are seen at these sites (Table 1), as well as in the Maritime Provinces (Morrison 1976).

TABLE 1
NUMBERS OF SEMIPALMATED SANDPIPERS CAUGHT DURING AUTUMN MIGRATION

Sampling site	Age	July 1–15	July 16–31	August 1–15	August 16–31	September 1–15
North Point, James Bay (1976)	Adults	369	3001	2778	661	3
	Juveniles	0	0	605	2381	473
Plymouth, Mass. (1973–77)	Adults	0	582	1001	319	27
	Juveniles	0	0	8	137	213

In New England and southeastern Canada the autumn migration of Semipalmated Sandpipers is more protracted than in spring, beginning in early July and continuing until early October. In the Montreal region, the peak of adults occurs at the very end of July, with the main passage of juveniles occurring around 20 August (S. Holohan, pers. comm.). In the upper Bay of Fundy at Mary's Point, N.B., numbers rise rapidly from mid-July and usually reach a peak at the end of July or in the first few days of August, remaining high into the first week of August (Morrison 1976). In Nova Scotia and Maine, small flocks arrive between early and mid-July, and numbers increase until the second week of August, when a sharp decline begins (Tufts 1973, Palmer 1949, Morrison 1976). The pattern of numbers at Plymouth, Mass., is apparently representative of northeastern sites in the U.S., with peak counts occurring in late July/early August. Highest numbers in New Jersey have been reported at the very end of July (Urner and Storer 1949, Kane 1976).

In the southeastern United States, peak counts of Semipalmated Sandpipers during autumn migration tend to be later and of lower numbers than at sites to the northeast, suggesting the possibility that many of the birds are juveniles. In Louisiana, peak numbers occur after early September (Lowery 1974), and in October/November in eastern Florida (Longstreet 1934). In northwestern Florida, Weston (1965) found practically no movement of Semipalmated Sandpipers during autumn, even though there is a very large westward movement along the Gulf Coast in spring. At Athens, Georgia, Burleigh (1958) rarely found the species in autumn, but found it comparatively often in spring.

Although abundant during autumn migration in the midwest, Semipalmated Sandpipers are less common than during spring (Oring and Davis 1966, Ferguson 1962, E. F. Martinez, pers. comm.).

MORPHOMETRIC STUDIES OF ADULT SEMIPALMATED SANDPIPERS

Bill and wing measurements

Breeding grounds.—Male Semipalmated Sandpipers tend to have shorter bills and wings than females (Ridgway 1919, Manning et al. 1956, Ouellet et al. 1973). Our own measurements of adults from a number of Canadian and United States museum collections (Table 2) confirm that males have shorter bills ($P < 0.01$) and shorter wings ($P < 0.01$) than females from the same area, and that Semipalmated Sandpipers from eastern breeding grounds tend to have longer bills than those from western areas. There is thus geographic as well as sexual variation in size, complicating morphometric analysis of data from live birds of unknown sex.

TABLE 2

Measurements of Museum Specimens of Semipalmated Sandpipers from Various Parts of the Breeding Range[a]

	Males				Bill/wing ratio		Females			
District[b]	$\bar{x}$[c]	N	(S^2)	CV	Males	Females	$\bar{x}$	N	(S^2)	CV
Bill length										
1. Alaska	17.27	23	0.53	4.24	.1853	.1964	18.92	9	0.17	2.18
2. Banks Island	17.53	7	0.95	5.56	.1859	.1980	19.68	5	0.44	3.36
3. Mackenzie district, NWT	17.76	5	0.46	3.81	.1881	.2037	19.20	4	0.53	3.78
4. Keewatin district, NWT	18.21	21	0.31	3.05	.1903	.2067	19.68[d]	5	0.71	4.87
5. W. Baffin Island	19.30	22	1.05	5.32	.2011	.2088	21.03	7	0.35	2.82
6. Belcher Is./E. Hudson Bay	19.99	20[e]	0.53	3.63	.2091	.2212	21.54	11[e]	1.11	4.88
Wing length										
1. Alaska	93.22	23	3.72	2.07			96.33	9	3.25	1.87
2. Banks Island	94.29	7	2.24	1.59			99.40	5	10.3	3.23
3. Mackenzie district, NWT	94.40	5	2.80	1.77			94.25	4	13.6	3.91
4. Keewatin district, NWT	95.67	9	3.25	1.88			95.20[d]	5	1.20	1.15
5. W. Baffin Island	95.95	22	4.43	2.19			100.71	7	0.57	0.75
6. Belcher Is./E. Hudson Bay	95.58	12	6.45	2.66			97.38	8	5.13	2.33

[a] All measurements by RIGM, except where noted.

[b] Numbers refer to collection areas illustrated in Figure 1.

[c] $\bar{x}$ = mean, N = sample size, S^2 = variance, CV = coefficient of variation.

[d] Measured by BAH; add 2 mm to wings to compare with measurements by RIGM.

[e] Includes measurements by BAH.

Spring migration.—Bill lengths of museum specimens collected at spring stopover areas (Table 3) in central and midwestern North America are shorter than those from eastern sites. For example, the average for 23 males from central and western areas (A, B, and C, Fig. 1, Table 3) is 17.9 mm, significantly shorter ($P < 0.01$) than the average (19.5 mm) for 56 males from eastern areas (E, F, and G, Fig. 1, Table 3). The same trend exists among females (Table 3). Reference to measurements of museum specimens from known breeding areas indicates that central and eastern migrants would be predominantly from western/central and eastern breeding areas, respectively.

Bill lengths of birds banded during spring migration followed the same trends as museum specimens, with lower averages at central and midwestern sites than at eastern sites (Table 4). For example, the average bill length in Kansas was 18.6 mm, much shorter than the comparable 21.1 mm from Massachusetts. The averages are statistically different ($P < 0.01$) for any of the comparisons possible between the spring samples in Table 4. Reference to museum measurements again indicates that migrants from the central U.S. breed in western/central areas, and eastern migrants breed in the eastern arctic.

The average wing length measurements of museum specimens increase from western to eastern breeding areas (Table 2), and in spring from western to eastern stopover sites (Table 3). Wing measurements from autumn migration sites were not compared because of the small number of specimens measured from central and midwestern locations.

Autumn migration.—As in spring, there is a trend for longer-billed birds to be found in eastern areas and for shorter-billed birds to be further west during

TABLE 3
MEASUREMENTS OF MUSEUM SPECIMENS OF SEMIPALMATED SANDPIPERS FROM VARIOUS MIGRATION AREAS[a]

		Males				Bill/wing ratio[c]		Females			
District[b]		$\bar{x}$[d]	N	(S^2)	CV	Males	Females	$\bar{x}$	N	(S^2)	CV
Bill length											
A. Alberta	spring[e]	17.39	8	1.03	5.84	.1826	.2052	19.90	4	1.15	5.40
	autumn[e]	17.47	3	0.14	2.17	.1865	—	—	—	—	—
B. Saskatchewan/ Manitoba	spring	18.12	5	2.38	8.51	.1895	.2014	19.80[e]	3	2.17	7.44
C. Central US[f]	spring	18.21	10	0.61	4.29	.1945	.2065	19.77	7	0.85	4.66
D. Maryland to Georgia	spring	19.59	14	1.13	5.44	.2029	.2188	21.40	26	1.38	5.49
	autumn	18.15	12	1.69	7.17	.1924	.2088	20.33	6	1.47	5.96
E. New York to Maine	spring	20.00	9	1.41	5.94	.2044	.2207	21.81	23	1.49	5.60
	autumn	19.50	13	1.92	7.10	.2044	.2068	20.13	12	4.10	10.06
F. Southern Ontario[g]	spring[e]	19.32	34	1.20	5.66	.2020	.2136	20.79	32	0.92	4.62
	autumn[c]	17.68	4	0.62	4.44	.1927	.2059	19.64	5	0.27	2.64
G. Kamouraska, St. Lawrence R., Quebec	spring	19.83	13	0.70	4.23	.2056	.2224	21.57	3	0.21	2.14
	autumn	18.78	16	0.71	4.48	.1954	.2014	19.81	8	1.45	6.08
H. Magdalen Is., Quebec	autumn	19.03	10	0.91	5.01	.2005	.2108	20.43	12	1.79	6.54
Wing length											
A. Alberta	spring[e]	95.25	8	16.79	4.30			97.00	4	3.33	1.88
	autumn[e]	93.67	3	6.33	2.69			—	—	—	—
B. Saskatchewan/ Manitoba	spring	93.60	5	1.30	1.22			98.33[e]	3	2.33	1.55
C. Central US[f]	spring	91.64	10	11.2	3.66			93.74	7	5.24	2.44
D. Maryland to Georgia	spring	94.56	14	1.57	1.33			95.79	25	5.40	2.43
	autumn	92.33	12	6.12	2.68			95.37	6	1.51	1.29
E. New York to Maine	spring	95.86	9	4.06	2.10			96.82	23	3.36	1.89
	autumn	93.41	12	4.81	2.35			95.33	12	14.24	3.96
F. Southern Ontario[g]	spring[e]	95.62	34	6.67	2.70			97.31	32	3.71	1.98
	autumn[e]	91.75	4	8.25	3.13			95.40	5	2.30	1.59
G. Kamouraska, St. Lawrence R., Quebec	spring	94.46	13	4.27	2.19			95.00	3	7.00	2.79
	autumn	94.11	18	2.34	1.63			96.38	8	3.41	1.92
H. Magdalen Is., Quebec	autumn	92.90	10	2.32	1.64			94.92	12	7.90	2.96

[a] Measurements by BAH, except where noted.
[b] Letters refer to collection areas illustrated in Figure 1.
[c] 2 mm added to wing measurements by BAH, to enable comparison with values in Table 2.
[d] $\bar{x}$ = mean, N = sample size, S^2 = variance, CV = coefficient of variation.
[e] Measured by RIGM; subtract 2 mm from wings to compare with measurements by BAH.
[f] Includes areas between the Mississippi River and Rocky Mountains.
[g] Includes areas between Toronto and Long Point.

autumn migration. Few comparisons can be made with museum specimens owing to the small number of autumn specimens from central and western migration areas. However, for samples of live, unsexed birds trapped during autumn banding, mean bill lengths in Kansas are significantly ($P < 0.01$) shorter than at eastern

TABLE 4

BILL LENGTH STATISTICS FOR SEMIPALMATED SANDPIPERS CAUGHT DURING SPRING AND AUTUMN MIGRATION

Sampling site	Spring migration				Autumn migration			
	N[g]	$\bar{x}$	SD	CV	N	$\bar{x}$	SD	CV
Quebec: Magdalen Is.[a]	—	—	—	—	169	21.00	—	—
Mass.: Plymouth[b]	204	21.1	1.39	6.58	1929	20.19	1.50	7.43
Ontario: James Bay, North Point[b]	81	20.6	1.29	6.25	6809	19.43	1.36	6.99
Virginia[c]	32	19.8	1.36	6.87	13	19.90	1.21	6.66
Ontario: Ottawa[d]	—	—	—	—	286	19.63	1.31	6.67
Ontario: Long Point[e]	—	—	—	—	22	18.85	1.06	5.60
Kansas: Cheyenne Bottoms[f]	77	18.6	1.18	6.32	201	18.16	1.21	6.08

[a] Data from Burton 1974.

[b] Data from this study.

[c] Spring data from Wallops Island, courtesy of Charles R. Vaughn; autumn data from Cedar Island, courtesy of John S. Weske.

[d] Data courtesy of Richard M. Poulin.

[e] Data courtesy of Michael S. W. Bradstreet.

[f] Data courtesy of E. F. Martinez.

[g] N = sample size, $\bar{x}$ = mean, SD = standard deviation, CV = coefficient of variation.

sites (Table 4), and means in Massachusetts are significantly longer than at Ottawa or James Bay ($P < 0.01$, Table 4).

Another striking feature of the autumn migration is that mean bill lengths of birds in a given area are consistently shorter than in the same area in spring, for both banding samples and museum specimens. For banding samples, autumn means were significantly shorter ($P < 0.05$) at all sites, except in Virginia where only small samples were available (Table 4). For museum specimens, mean bill lengths of both males and females in eastern areas were up to 1.5 mm shorter in autumn than in spring, and comparison of samples over 10 birds showed the differences were statistically significant ($P < 0.01$). Similar trends were found with wing lengths (Table 3). The consistent decrease at all eastern sites, involving both sexes, indicates that many birds from western and central arctic breeding areas migrate southwards via the Atlantic coast in the autumn.

Means for both bill length and wing length decrease during the course of autumn migration in Semipalmated Sandpipers trapped in James Bay, 1975–76 (N = 8986), and at Plymouth, Mass., 1973–1977 (N = 1929) (Fig. 2). The large difference in wing measurements between sites is accounted for almost entirely by differences in measuring technique (see Methods). Bill lengths are consistently lower in James Bay than in Massachusetts, indicating that fewer eastern arctic birds are present in James Bay. Seasonal decreases in wing and bill length could be caused at least partly by an earlier migration of larger female birds, as would be anticipated from consideration of the species' breeding biology (Pitelka et al. 1974). However, other evidence presented below indicates that an increasing proportion of small birds from more westerly breeding areas also contributes to the decline as the migration proceeds.

Bill/wing ratios of adults

Breeding grounds.—The mean bill/mean wing ratio increases for both males (from approx. 0.185 to 0.210) and females (from approx. 0.195 to 0.220) from western to eastern breeding areas (Table 2, Fig. 3). Males from the Alaskan and

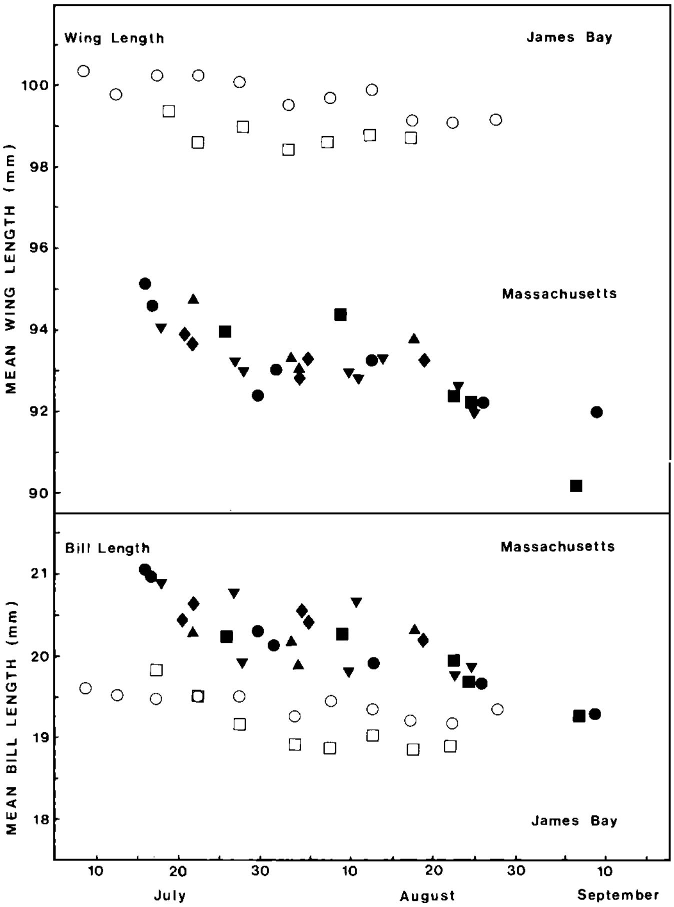

FIGURE 2. Mean wing lengths and mean bill lengths of Semipalmated Sandpipers captured at North Point, James Bay (□—1975, N = 2177; ○—1976, N = 6809), and Plymouth, Mass. (▼—1973, N = 520; ●—1974, N = 492; ▲—1975, N = 214; ◆—1976, N = 366; ■—1977, N = 377), during autumn migration. Points for Plymouth represent single catches, whereas those for James Bay represent means of 5-day periods. Note that means of both wing and bill fall during the passage. The large difference in wing length between sites is accounted for almost entirely by difference in measuring techniques. Bill lengths are, however, comparable and are consistently lower in James Bay than in Massachusetts, indicating the latter site probably receives a higher proportion of birds from eastern breeding areas.

central populations form a group with bill/wing ratios of ca. 0.185 to 0.190 at mean bill lengths of ca. 17.3 to 18.2 mm, whereas males from the eastern populations are grouped with bill/wing ratios between 0.20 and 0.21 and mean bills between 19.3 and 20.0 mm, respectively. Western and central area females broadly overlap the eastern male group (ratios 0.196 to 0.207 at bill lengths of 18.9 to 19.7 mm), but are themselves separated from females from eastern areas (ratios 0.209 to 0.221 at bill lengths of 21.0 to 21.5 mm). The separation of Alaskan/central and eastern (Baffin Island and northern Quebec) populations into two distinct groups (where the sex is known) is consistent with the suggestion of Manning et al. (1956) that there is possibly a discontinuity or step in the cline in the vicinity of

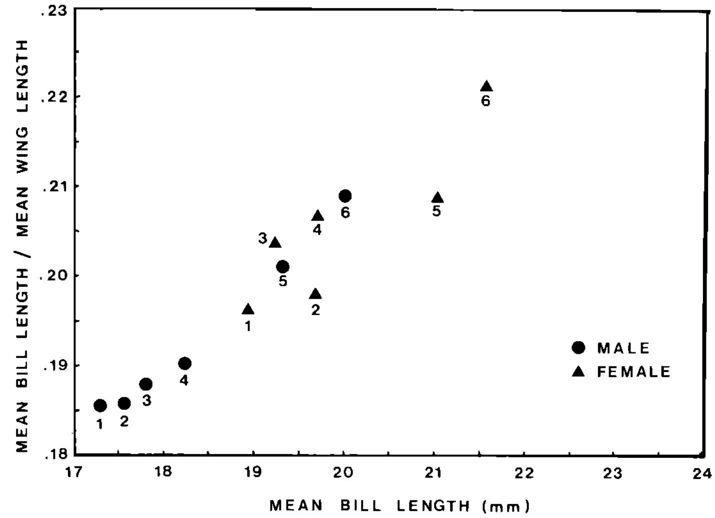

FIGURE 3. Mean bill length/mean wing length ratio vs. mean bill length for Semipalmated Sandpipers from different parts of the breeding range. Circles = males, triangles = females; numbers refer to areas illustrated in Figure 1. Birds from Alaskan (area 1)/central (2–4) and eastern (5, 6) parts of the breeding range form two groups for males and females, respectively, with eastern males and Alaskan/central females generally overlapping.

Southampton Island. Examination of the bill/wing ratio vs. mean bill length may thus be of value in establishing the possible breeding origin of migrants in museum collections where sexed samples are available.

Spring migration.—Plots of bill/wing ratio vs. mean bill length for males and females collected during spring migration from various areas are illustrated in Figure 4. Males collected during the spring in Alberta fell at the lower end of the Alaskan/central group, indicating most birds were probably from Alaskan or western arctic breeding areas. Males from the central U.S., comprising areas between the Mississippi River and the Rocky Mountains, and from southern Saskatchewan/Manitoba fell nearer the upper end of the Alaskan/central group, suggesting that most of them were from central parts of the breeding range. Males collected from areas along the eastern U.S. seaboard (New York, New England and Maryland to Georgia), the St. Lawrence River (Kamouraska, Quebec) and in southern Ontario all fell well within the range of values of males from eastern breeding areas.

Females collected in the central U.S., Alberta and Saskatchewan/Manitoba fall near the group from Alaskan and central breeding areas, whereas migrant females from the eastern coast of the U.S. and the St. Lawrence River fall well toward the upper end of the group from the eastern arctic, with southern Ontario migrants nearer the lower end of the group (Fig. 4).

These results demonstrate that birds passing through eastern areas of North America in spring are principally from breeding areas in the eastern arctic, and that those from central and western areas of the breeding grounds use interior migration routes through the central U.S. and Canada.

Autumn migration.—For areas in eastern North America, bill/wing ratios of migrant Semipalmated Sandpipers are generally lower in the autumn than in the

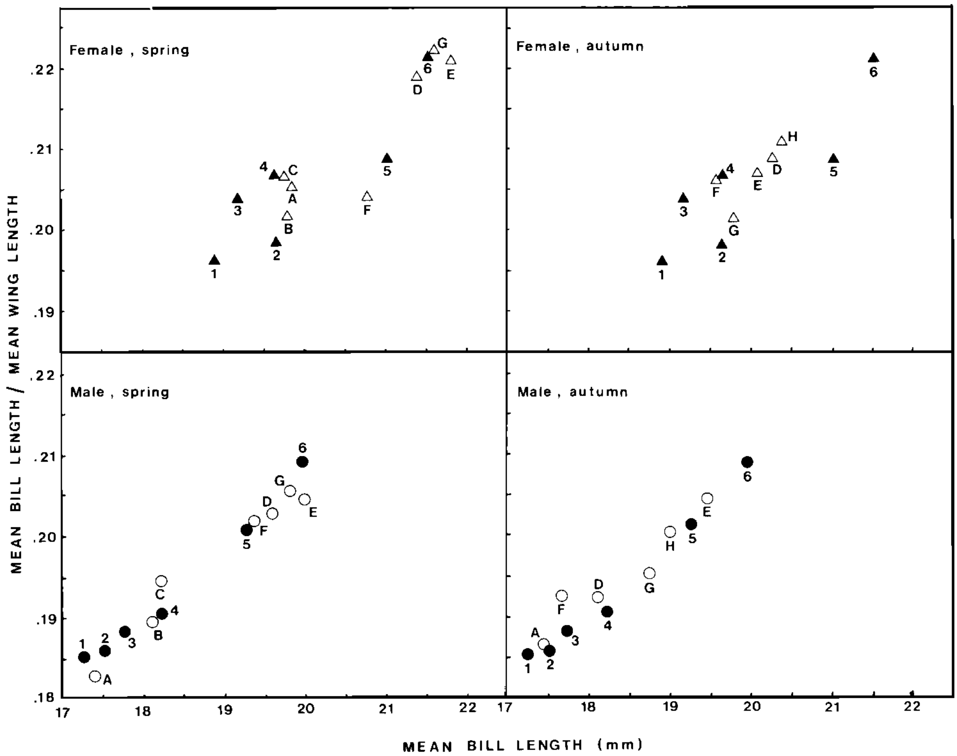

FIGURE 4. Mean bill length/mean wing length ratio vs. mean bill length for male and female Semipalmated Sandpipers collected in migration areas (open symbols, letters) during spring and autumn in North America. Reference points for samples from different parts of the breeding range (solid symbols, numbers, see Figure 3) are included. Numbers and letters refer to areas illustrated in Figure 1. Note that in spring, males and females using central migration routes (areas A, B, C) appear to derive principally from Alaskan/central populations, whereas those from the Atlantic seaboard and eastern Canada (areas D, E, F, G) are principally from eastern breeding areas. In the autumn, many western/central arctic birds would appear to use sites on the eastern seaboard (see text for details).

spring for both males and females (Table 3, Fig. 4), providing further evidence that many birds from central and possibly western breeding areas migrate to their wintering areas via the Atlantic seaboard. The effect appears to be least pronounced towards the edges of the migration corridor and most pronounced towards the middle, and may be partly seasonally dependent. Thus, bill/wing ratio vs. mean bill points for autumn males in Alberta fall well within the Alaskan/central group, indicating most birds are from western breeding areas, as in spring (Fig. 4). On the east coast, males collected in the Magdalen Islands (August) and NY/New England areas (July/August) fall closest to the eastern breeding group, with bill/wing vs. mean bills for females falling between the eastern and Alaskan/central groups, indicating a relatively high proportion of eastern birds on the north and eastern sections of the Atlantic seaboard.

Males collected during August between Maryland and Georgia have bill/wing vs. mean bill plots close to the group from Alaskan/central breeding areas, indicating a high proportion of birds from those areas, in contrast to the spring when the majority of birds appeared to be from eastern breeding areas. Measurements

TABLE 5

Coefficients of Variation for Bill Lengths of Semipalmated Sandpipers Collected in Arctic Breeding Areas, and for Combinations of Samples from Different Areas

	Males		Females		Males + Females	
Area[a]	CV	*N*	CV	*N*	CV	*N*
A	4.43%	53	3.02%	33	6.54%	86
B	3.98	33	3.70	14	5.46	47
C	4.84	42	4.30	18	6.08	60
A + B	4.59	86	3.43	47	5.90	133
B + C	6.22	75	5.96	32	7.25	107
A + C	7.70	95	6.63	51	8.21	146
A + B + C	7.00	128	6.14	65	7.70	193

Statistical comparison (*t*-test) of coefficient of variation for bill lengths of mixed sex samples from different breeding zones, and of combinations of samples from different breeding zones.

	A + B	B + C	A + C	A	B	C
A	n.s.	$P < 0.05$	$P < 0.001$	—	—	—
B	n.s.	$P < 0.01$	$P < 0.001$	n.s.	—	—
C	n.s.	n.s.	$P < 0.01$	n.s.	n.s.	—

[a] The areas are combinations of samples from Table 2 grouped to represent: (A) Alaskan arctic (area 1 in Fig. 1); (B) central Canadian arctic (areas 2–4 in Fig. 1); and (C) eastern Canadian arctic (areas 5 and 6 in Fig. 1).

of females from the Maryland/Georgia coast, and of both males and females collected in southern Ontario (July/September) and Kamouraska on the St. Lawrence estuary (August), indicate the presence of many western/central birds in the latter areas during the autumn, particularly late in the season, consistent with the observations of Manning et al. (1956) who noted that the culmen/bill width ratios of 11 migrants collected at Tadoussac, Quebec (July/August) indicated the birds were from western breeding areas, an interpretation also suggested by Ouellet et al. (1973).

Bill/wing ratios of birds trapped in James Bay and Massachusetts fall during the period of autumn migration (not illustrated). Little seasonal information could be obtained from museum specimens owing to small sample sizes, though the available material from the New York area indicated a decline in bill/wing ratios vs. mean bill for both males and females between July and August. These results again suggest that seasonal decreases are not caused simply by changing sex ratios but by an increasing proportion of birds from central and western breeding areas.

Coefficient of variation

Breeding grounds.—The coefficients of variation (CV) for samples of breeding adult Semipalmated Sandpiper bill lengths are given in Table 5. The values are lowest within samples of one sex from one breeding zone (range 3.02–4.84% in Table 5), being higher (i) in samples of one sex from different breeding zones (3.43–7.70%), (ii) in samples of both sexes from one zone (5.46–6.54%), and (iii) most of all in samples of both sexes from different breeding areas (5.90–8.21%). The CV values from any one region in Table 5 are not significantly different from those of any other single region. Statistical differences occur only when a single region is tested against two or more regions combined, providing the combination includes birds from the eastern arctic (Table 5).

Spring migration.—The CVs from museum samples are directly comparable to values obtained from live birds, because they are based upon measures of relative rather than absolute variation.

The CV values found for bill lengths in samples of live sandpipers caught during spring are not significantly different between stopover sites (Table 4); each is within the range expected in a randomly selected, sexually mixed sample drawn from a relatively narrow portion of the breeding range (Table 5). For example, the highest spring value, 6.25% from James Bay, is not significantly different ($t = 1.06$, $P < 0.30$, 126 df) from the lowest value (5.46%) among the museum groups representing breeding areas (Table 5).

Autumn migration.—CV values were higher during autumn than during spring migration at each site where samples of 30 or more birds could be compared (Table 4), though the difference was statistically significant only in Massachusetts ($t = 2.45$, $P < 0.05$, 2131 df). At James Bay and in Massachusetts, two areas where autumn monthly sample sizes can be compared, the CVs were lower in July than in August. The James Bay CV during July 1976 was 6.81% ($N = 3{,}370$), close to the spring value and to the values found in mixed-sex samples from single portions of the breeding range (Table 5). In August, the James Bay CV was 7.14% ($N = 3439$), significantly higher ($t = 2.76$, $P < 0.01$) than in July, and similar to values found for mixed-sex groups combined from more than one part of the breeding range (cf. Table 5). At Plymouth, the July ($N = 582$) and August ($N = 1337$) CVs were 6.59% and 7.71% respectively ($t = 4.59$, $P < 0.001$). These changes in CVs at both sites suggest a larger geographic representation at autumn stopover areas in August than in July, or than found in spring.

DISCUSSION

Our results corroborate evidence that Semipalmated Sandpipers use different routes for north and south migration (Cooke 1910, Loftin 1962, McNeil et al. 1973, 1977). The migration strategy is more complex than previously understood because it is not the same for birds from different parts of the breeding range. We have divided the breeding range into three general areas, Alaskan arctic (area 1 in Fig. 1), central Canadian arctic (areas 2–4 in Fig. 1), and eastern Canadian arctic (areas 5–6 in Fig. 1).

Alaskan Semipalmated Sandpipers apparently follow a north migration route through the Great Plains region of the United States and Canada, judging from the short average bill lengths in live samples caught in Kansas (Table 4) and the generally short bill lengths in museum specimens collected in the Great Plains (Table 3). The bill/wing ratios of Alaskan and central breeders are also similar to those specimens collected during spring in the Great Plains (Fig. 4).

In autumn many Alaskan Semipalmated Sandpipers retrace the North American portion of their spring route. An additional, unknown proportion may also use routes farther east, a possibility we cannot accurately resolve. Evidence for the first part of this conclusion comes partly from banding and morphometric studies in Kansas by E. F. Martinez. The average bill length in autumn at Cheyenne Bottoms is short (Table 4), and the CV is low, both results suggesting that Alaskan breeders are involved. One bird banded during spring in Kansas has been recovered on the Alaskan North Slope and two birds banded at Barrow, Alaska, were subsequently trapped at Cheyenne Bottoms (Martinez 1974). A number of Semipalmated Sandpipers banded during spring in Kansas have been recaptured at the same site in autumn (Parmelee et al. 1969, Martinez, pers. comm.).

Semipalmated Sandpipers that breed in eastern Canadian arctic regions apparently migrate north by an Atlantic route on the United States seaboard, probably turning cross-country in the northeastern United States and southeastern Canada. Evidence for this view includes the long average bill lengths found in samples caught for banding in Massachusetts (Table 4) as well as the long averages from specimens collected in New England and Quebec (Table 3). The low CV values in the Massachusetts banding samples indicate a mixed-sex sample from one geographic region which, because of the bill lengths, could only be the eastern region. Bill/wing ratios of migrants in eastern areas again indicate spring migrants are en route to eastern arctic breeding areas (Fig. 4). The western margin of the migration corridor for eastern birds is not clear. The spring bill/wing ratios (Table 3) from southeastern sites are similar to the values farther northeast, indicating that spring migrants there are from eastern breeding areas. However, the significantly ($P < 0.001$) lower average bill length of the spring sample in Virginia compared to Massachusetts makes this conclusion somewhat less clear. A sexual bias (more males) in the Virginia banding sample could account for the difference. The relatively low CV would be unlikely if the sample included both sexes from central and eastern breeding areas, reinforcing the possibility of a sexual sampling bias.

The point at which the autumn route of eastern Semipalmated Sandpipers crosses the North American Atlantic seaboard apparently is somewhat north and east of the spring route. The average bill lengths, CV values from banding samples (Table 4) and bill/wing ratios from museum collections (Fig. 4) indicate the presence of eastern breeders in a zone along the east coast between Chesapeake Bay and the Gulf of St. Lawrence, with highest proportions of eastern birds in samples from northern stations. These conclusions are supported by banding and other studies at the mouth of the St. Lawrence estuary (cf. McNeil and Burton 1973, 1977, McNeil and Cadieux 1972), which show that many of the sandpipers that visit the Magdalen Islands launch a transoceanic flight to Caribbean islands. An unknown proportion travel southwest from the Magdalen Islands in a coastwise movement to the Maritimes, but relatively few continue further south along the coast of the United States (McNeil and Burton 1973, 1977, Morrison 1977a). These results agree well with the morphometric studies described here. The bill length averages in Massachusetts (Table 4) are shorter in autumn than in spring, suggesting a lower proportion of long-billed, eastern birds. The high CV values in autumn (Table 4) indicate the presence of eastern breeders, as well as birds from other regions.

Taken together, evidence shows that the majority of eastern Semipalmated Sandpipers use an autumn migration route over eastern North America that passes to sea in a zone centered in southeastern Canada. International shorebird surveys organized jointly by the Canadian Wildlife Service and the Manomet Bird Observatory, Massachusetts, have shown that by far the highest numbers of Semipalmated Sandpipers on the Atlantic seaboard in autumn occur in this zone, particularly in the upper Bay of Fundy (Morrison 1977a). This route lies slightly north and eastward of the one used for spring migration.

The migration routes used by Semipalmated Sandpipers from the central Canadian arctic come closest to conforming to the concept of an elliptical migration route involving a northerly passage through the central U.S. followed by an autumn migration across the Atlantic seaboard (see McNeil 1970, McNeil and Burton 1973, 1977). Morphometric and banding data indicate a spring passage across the Gulf of Mexico and north through central North America in a zone between the Rocky Mountains and the Appalachian mountains. In Kansas, the higher average bill length in spring than in autumn (Table 4) is probably caused by the mixing of central arctic with Alaskan birds in spring but not in autumn. Such mixing probably would not increase the CV significantly unless eastern Canadian birds were involved (Table 5).

Current information does not allow testing whether some central Canadian birds might also arrive on the southeast Atlantic coast in spring and then pass overland, possibly via Appalachian water gaps or other routes. If this does happen, few birds reach as far north as Massachusetts, judging from the high average bill length and the low CV value found there (Tables 3 and 4).

In autumn, central Canadian Semipalmated Sandpipers appear to migrate east of their spring routes, thus accounting for the lower average bill length than in spring in the banding samples at James Bay and Plymouth (Table 4) and in all the eastern groups of museum specimens (Table 3). The bill lengths found at James Bay (Figure 2) suggest that the majority of Semipalmated Sandpipers there are from central breeding regions, though the presence of some eastern birds is indicated by the high CV values (Table 4). The proportion of eastern birds must be low by comparison to Massachusetts where average autumn bill lengths are significantly longer (Fig. 2, Table 4). To summarize, the morphometric information indicates that central Canadian birds travel southwards in a corridor that intersects the Atlantic coast in a zone between the Gulf of St. Lawrence and Virginia, occurring in lower proportions from Massachusetts northwards, and in higher proportions south of Massachusetts.

Banding evidence shows that many Semipalmated Sandpipers travel north through the central United States and Kansas, and south via eastern corridors including the James Bay and Atlantic coasts (Anderson 1968, Parmelee et al. 1969, Martinez 1974 and pers. comm.), thus agreeing well with the morphometric data. In addition, color-marking work carried out at North Point, James Bay, has resulted in numerous sightings of Semipalmated Sandpipers in a coastal zone between the St. Lawrence estuary and Virginia. A much higher proportion of sightings occurred in the United States sector of this zone from work in James Bay than from similar studies on the Magdalen Islands (McNeil and Burton 1973, 1977; Morrison 1977a, b, 1978).

Our results indicate that different migration strategies are used by Semipalmated Sandpipers from the eastern and western parts of the breeding range. The somewhat earlier northward movement of Alaskan/central populations through the Great Plains appears to be influenced by climatic factors. Surface winds are generally southerly along the coast of the Gulf of Mexico and in the southern central parts of the U.S. between March and May (Bryson and Hare 1974, Court 1974), and western areas further north, including inland Alaska, generally warm up earlier than eastern areas at equivalent latitudes, leading to an earlier thaw (Hare and Hay 1974). In some years short-billed migrants have virtually completed their passage through midwestern areas and started arriving in Alaska in late May (Bailey 1948, Gabrielson and Lincoln 1959, Irving 1960), a time when peak passage of long-billed birds on the east coast is just beginning.

During July and August, marine invertebrate food resources are likely to be at their peak in east coast estuaries, and the prevailing airflow patterns are from the northwest (Bryson and Hare 1974). Many birds from eastern and central breeding areas thus appear to have adopted an autumn migration strategy involving a flight to staging areas on the Atlantic seaboard, followed by a transocean flight to wintering grounds in South America. Most Alaskan birds, on the other hand, appear to retrace their spring route, moving southward through the interior. It is not clear whether this overland section is accomplished in a series of relatively short flights or by long stages, nor where the principal wintering grounds may be, though areas in Central America and on the west coast of South America appear probable. It also seems possible that the molt strategy of the Alaskan birds may differ from those from eastern areas (E. F. Martinez, pers. comm.).

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SEASONAL HABITAT USE BY ARCTIC ALASKAN SHOREBIRDS

P. G. CONNORS, J. P. MYERS, AND F. A. PITELKA[1]

ABSTRACT.—Shorebirds display a wide range in seasonal patterns of habitat use along the arctic coast near Point Barrow, Alaska. Differences between species reflect habitat preferences, the timing of movements with respect to seasonal habitat availability, and whether the use is breeding, post-breeding, or migrational. During the breeding season (June and July), most activity is centered on the tundra, but by early August a marked coastal movement occurs, resulting in high densities of particular species in shoreline and adjacent habitats. In August and September, widespread use of littoral habitats develops, especially for such species as Red Phalarope, Ruddy Turnstone, and Sanderling. In contrast, Golden Plovers and Pectoral Sandpipers restrict most of their activities to the tundra. Other species exhibit intermediate patterns of habitat use. These patterns determine the dependence of each species on arctic coastal habitats, and the susceptibility of each species to disturbances related to outer continental shelf oil development.

Shorebirds comprise a major portion of the avifauna along the Beaufort and Chukchi coasts of arctic Alaska (Bailey 1948, Gabrielson and Lincoln 1959, Pitelka 1974). In fact, their breeding distributions are restricted in large part to arctic and subarctic regions (Palmer 1967). Moreover, on the coastal plain, they collectively are responsible for most of the insectivory in tundra trophic dynamics. This implies a strong dependence on environmental conditions prevailing within the region, and compels us to examine possible ways that the escalating development of North Slope energy resources may affect shorebird populations. A species list is provided in Table 1.

Much of the current development is oil-related, both on the coastal plain at Prudhoe Bay, Alaska, and spreading westward toward Barrow and inland over the Naval Petroleum Reserve area. Increasing activity focuses on extracting oil from the outer continental shelf. Use of natural gas deposits is also anticipated, and in the future mining coal may become an important activity. Because each of these developments will have different centers of activity and different environmental effects, their importance to shorebird populations will vary, influenced by changing patterns in habitat use by arctic coast species. An essential step in identifying possible consequences of development therefore involves examining seasonal changes in habitat use: How do different species use the arctic coast environment, and what effects do their use patterns have on susceptibility to oil-related disturbances?

In this paper we examine general patterns in habitat use by shorebirds common near Barrow, Alaska. Data were gathered during 1975 and 1976 on a series of transects constructed in littoral (shoreline) and tundra habitats in the Barrow area. The patterns suggest a preliminary classification of North Slope shorebirds in terms of their sensitivities to development activities.

STUDY AREA

Point Barrow (latitude 71°23′N, longitude 156°28′W) is the northernmost point on a gravel spit 12 km long marking the boundary between Beaufort and Chukchi seas (Fig. 1). The area around Point Barrow offers a diverse set of lowland habitats, including both littoral areas and tundra. Littoral habitats include brackish water mudflats and marsh pools, mud and gravel shores of sloughs and

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TABLE 1

SHOREBIRD SPECIES OCCURRING REGULARLY ALONG THE BEAUFORT AND CHUKCHI COASTS OF ALASKA

Regular Breeders

Semipalmated Plover, *Charadrius semipalmatus*
American Golden Plover, *Pluvialis dominica*[a]
Black-bellied Plover, *Pluvialis squatarola*
Ruddy Turnstone, *Arenaria interpres*[a]
Black Turnstone, *Arenaria melanocephala*
Common Snipe, *Capella gallinago*
Whimbrel, *Numenius phaeopus*
Red Knot, *Calidris canutus*
Pectoral Sandpiper, *Calidris melanotos*[a]
White-rumped Sandpiper, *Calidris fuscicollis*
Baird's Sandpiper, *Calidris bairdii*[a]
Dunlin, *Calidris alpina*[a]
Semipalmated Sandpiper, *Calidris pusilla*[a]
Western Sandpiper, *Calidris mauri*[a]
Stilt Sandpiper, *Micropalama himantopus*
Buff-breasted Sandpiper, *Tryngites subruficollis*
Long-billed Dowitcher, *Limnodromus scolopaceus*[b]
Bar-tailed Godwit, *Limosa lapponica*
Red Phalarope, *Phalaropus fulicarius*[a]
Northern Phalarope, *Lobipes lobatus*

Additional Migrants

Killdeer, *Charadrius vociferous*
Sharp-tailed Sandpiper, *Calidris acuminata*
Least Sandpiper, *Calidris minutilla*
Rufous-necked Sandpiper, *Calidris ruficollis*[c]
Curlew Sandpiper, *Calidris ferruginea*[c]
Sanderling, *Calidris alba*[b,c]
Hudsonian Godwit, *Limosa haemastica*

[a] Eight species common as breeders near Barrow.
[b] Two species common as migrants near Barrow.
[c] Also known to breed occasionally at least near Barrow.

lagoons, and gravel ocean beaches. In the absence of storms, vertical tidal fluctuations are less than 30 cm, and horizontal water line movement is almost undetectable. Occasional wind-driven tides maintain salt marsh and brackish pool habitats above the normal water line. In general, wave action is slight because of the influence of sea ice. The tundra is highly polygonized, and varies from low wet marshes to drier ridges with occasional wet troughs and no more than 2–3 m higher than the neighboring lowlands. Tundra vegetation and landforms in the study area are described in Britton (1957).

METHODS

Marked transects were established throughout the study area in a wide range of littoral and tundra habitats accessible within 20 km of Point Barrow. In littoral areas we censused 22 transects, totaling 18.4 km long by 50 m wide along shorelines and 2.3 km long by 100 m wide on mudflats and salt marsh areas, for a total littoral transect area of 115 ha; on the tundra we censused 10 transects, each 1 km × 100 m wide, total area of 100 ha. All transects were censused at least once during each 5-day period from 1 June 1976 through 17 September 1976. A smaller set of transects was censused similarly from 30 June 1975 through 2 September 1975. In this paper we analyze data only from the more complete 1976 season.

We present the data in two ways: (1) To describe the overall pattern of habitat use by Barrow shorebirds and to consider individual species' movements we use actual transect census totals. Total

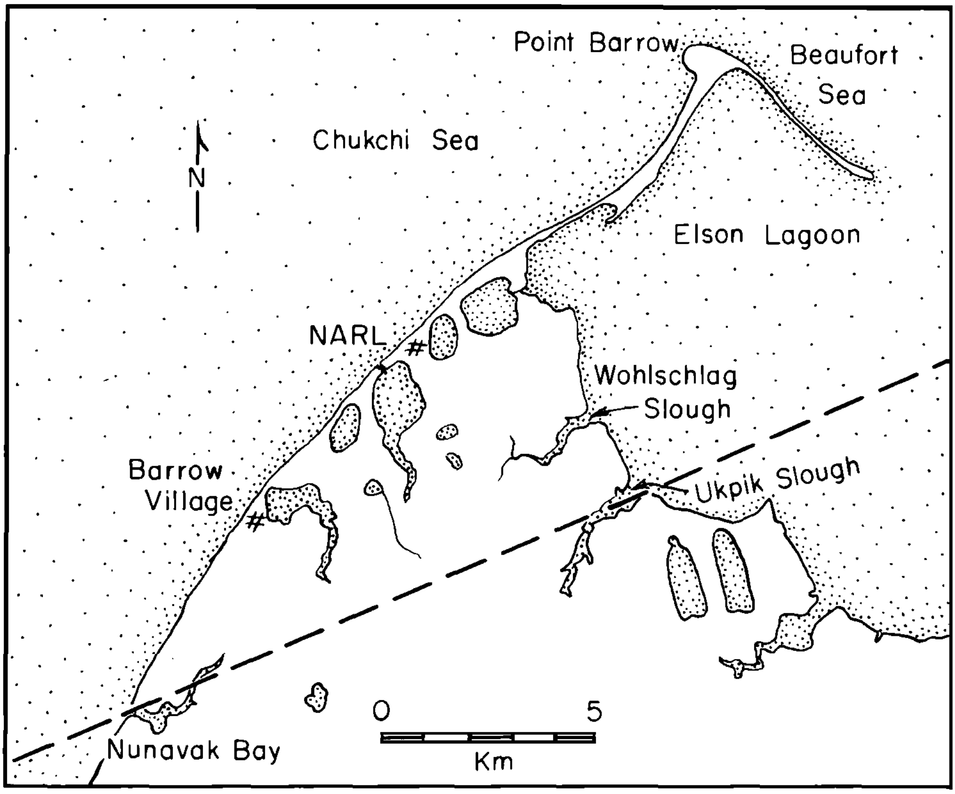

FIGURE 1. Map of study area near Point Barrow, Alaska. Habitats sampled by transects are all north of the dashed line.

areas of littoral and tundra transects are comparable (115 ha vs. 100 ha, respectively), so these data approximate areal densities. We do not use densities in this case because of spatial differences in bird use between habitats: Along shorelines most shorebird activity is concentrated within a narrow strip and is best calculated as a linear density; in contrast, mudflat and tundra habitats require areal densities. Because transect dimensions in both habitats remained constant throughout the season, transect census totals allow seasonal comparisons in use of tundra and littoral habitats; at the same time they show directly the numbers of individuals occurring along our transects.

(2) To examine the importance to birds of tundra vs. littoral habitat we calculate an index of relative littoral use, U_L, which corrects for the difference in areal extent between these two habitat categories within the local Barrow study area. For this calculation the region of interest lies north of a line from Nunavak Bay to Ukpik Slough (Fig. 1). Using a shoreline width of 50 m (width used for censusing), the ratio of total tundra to total littoral habitat is 12.9. The relative use of littoral habitat, U_L in the Barrow area is defined as

$$U_L = \frac{D_L}{D_L + 12.9D_T},$$

where D_L = density in littoral habitat and D_T = density in tundra habitat. The correction factor (12.9) is sensitive to the position of the line used to define the region of interest. We placed it as indicated in Figure 1 in order to include only the area sampled by our transect arrays. The index, U_L, thus reflects the importance of littoral habitats only in relation to the immediately adjacent tundra.

RESULTS

The census data yield a phenology of habitat use in the Barrow area. In this preliminary treatment we make only one habitat distinction, categorizing tran-

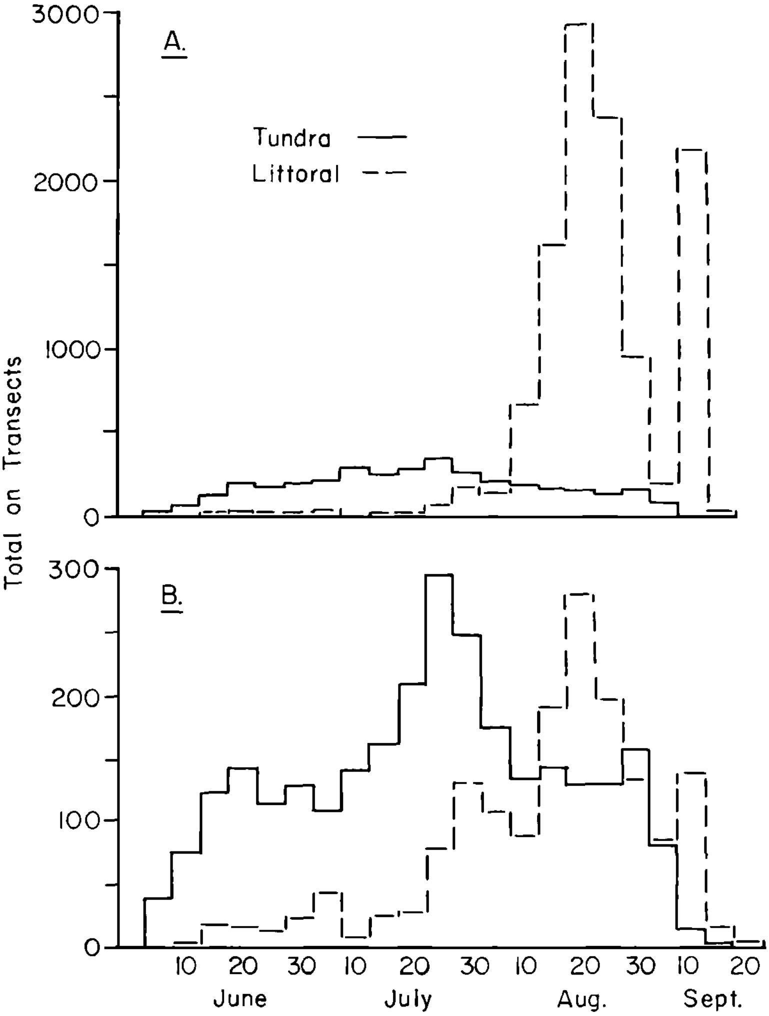

FIGURE 2. Seasonal habitat use, tundra vs. littoral, for all shorebirds combined (A) and for all shorebirds except Red Phalaropes (B).

sects as either littoral or tundra. Subsequent papers will consider changing patterns within tundra and littoral zones in more detail.

During the nesting period in June and July, activity centers on the tundra (Fig. 2). Shorebirds' main prey base during this interval consists of freshwater zooplankton and insect larvae and adults (Holmes and Pitelka 1968). As juveniles fledge in late July and August, shorebirds occur on mudflats, lagoon edges, and ocean shorelines in increasing numbers, shifting to a diet of oligochaetes and insect larvae on mudflats and a wide variety of marine zooplankton along the shore (Connors and Risebrough 1977). By mid-August the littoral zone becomes a major foraging area for many species. This situation continues through early September, after which time few shorebirds remain in the Barrow area. The switch from tundra to littoral resources occurs in parallel with an increased avail-

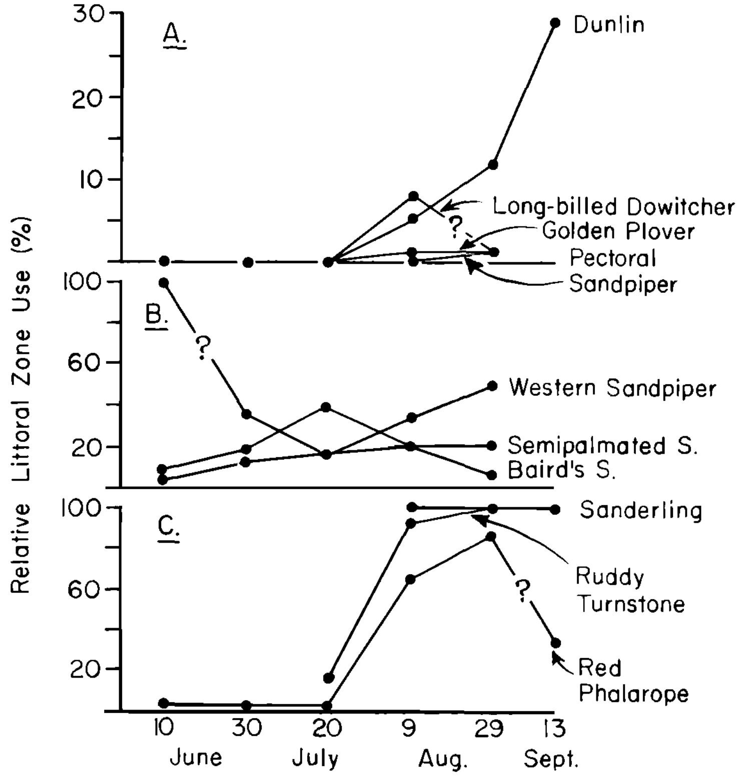

FIGURE 3. Relative use of littoral habitats by shorebird species in study area (see text). A includes species from categories I and II, Table 2; B corresponds to category III, C to category IV.

ability of littoral habitat. Prior to July sea ice effectively precludes birds from using most marine shoreline habitats.

The overall seasonal pattern in Figure 2 actually consists of several distinct habitat use patterns representing the responses of particular species to the mosaic of arctic coastal habitats near Barrow. The species comprising the shorebird community differ with respect to their seasonal use of littoral and tundra habitats.

TABLE 2
HABITAT USE PATTERNS OF COMMON SHOREBIRDS NEAR BARROW, ALASKA

Category	Breeding	Post-breeding adult	Post-fledging juvenile	Species
I	T[a]	T	T	Golden Plover, Pectoral Sandpiper
II	T	T + L	T + L	Dunlin, Long-billed Dowitcher
III	T + L	T + L	T + L	Western, Semipalmated, Baird's Sandpipers
IV	T	T + L	L	Red Phalarope, Ruddy Turnstone, Sanderling

[a] T, tundra; L, littoral.

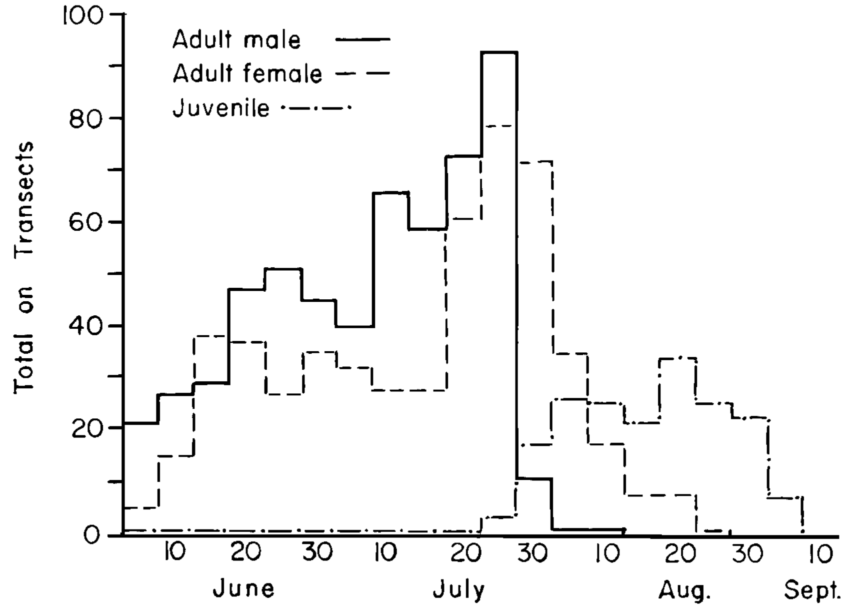

FIGURE 4. Seasonal use of tundra habitats by Pectoral Sandpipers.

This can be seen in Figure 3 which presents the relative use of littoral habitat, U_L (see Methods), during successive 20-day periods throughout the summer.

Species vary in the extent to which they move to littoral habitats. Some, such as Golden Plovers, never leave the tundra, while others, for example Ruddy Turnstones, switch almost entirely. Between these extremes are several intermediate patterns varying in extent and timing of the littoral movement. Part of this variation results from differential movement of age and sex classes to littoral habitats. Table 2 presents four categories of seasonal habitat use patterns, based on these considerations, which summarize interspecies variation. The same four categories are suggested by the 20-day period comparisons in Figure 3.

Category I includes Golden Plovers and Pectoral Sandpipers, the two species most restricted to tundra habitats throughout the summer season. Both appear only sparingly in the littoral zone near Barrow, despite major migrational buildups on the adjacent tundra. Pectoral Sandpipers, for example, show progressive movements of post-breeding males, post-breeding females, and fledged juveniles at tundra sites (Fig. 4), yet only occasionally do individuals appear on littoral transects (Fig. 3A).

Members of Category II confine their breeding activities to the tundra, but include significant use of both habitats during subsequent periods. Dunlins exhibit this pattern: In June and early July, Dunlins use tundra resources almost exclusively. As littoral sites become available, post-breeding adults and fledged juveniles occur increasingly in these habitats. Throughout the summer, however, Dunlins continue to exploit tundra habitats. Long-billed Dowitchers are uncommon as breeders near Barrow, but a substantial movement of migrating juveniles in August, highly variable from year to year, occurs in both habitats.

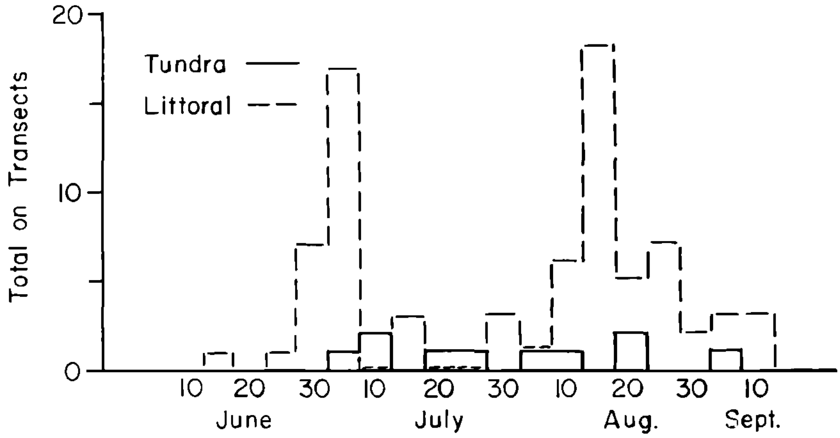

FIGURE 5. Seasonal habitat use, tundra vs. littoral, by Western Sandpipers.

Species in Category III utilize littoral as well as tundra habitats near Barrow during the breeding season, and post-breeding migrational movements occur in both habitats. Western Sandpipers (Fig. 5) and Semipalmated Sandpipers (Fig. 6) occur in littoral areas throughout the breeding season, foraging along stream sloughs, mudflats, and lagoon edges near their tundra nesting sites. The Western Sandpiper exhibits a late June, early July peak of apparently non-breeding adults, and a mid-August peak of migrating juveniles, both heavily littoral. Semipalmated Sandpiper densities are fairly constant through the breeding season in both habitats, with a build-up of migrating adults in late July followed by a sudden and very sharp peak of migrating juveniles around August 1. This juvenile movement is striking. The peak is actually sharper than shown in Figure 6, since this graph averages a very high and a very low count within the August 1 period. In both 1975 and 1976, juveniles appeared along lagoon shores and on mudflats as a sudden wave, with densities dropping a few days later. Figures 5 and 6 also indicate that the juvenile migrational peaks of these two ecologically similar species occur at different times, offset by 5 to 10 days, greatly reducing the overlap in time of their occurrences on the limited mudflats near Barrow. A third species within this category, Baird's Sandpiper, nests in a variety of habitats near the coast at Barrow, ranging from tundra high polygons to (occasionally) gravel beaches. As Figure 3B indicates, it occurs in littoral and tundra habitats throughout the season.

Species in Category IV shift from almost exclusive use of tundra for breeding to heavy dependence on littoral areas by post-fledging juveniles (Fig. 3C). Figure 7 presents the seasonal occurrence of different Red Phalarope age and sex classes on tundra transects. In early June, adult males and females increase in density in a 1:1 ratio, but associate only until clutches are completed. In late June and early July, females abandon nests and flock together as southward migration begins. Males incubate and attend the young until the latter are nearly fledged, at which time the males begin to flock and leave the Barrow region. Fully fledged young then begin a dramatic movement to littoral areas, as reflected by the August peak in Figure 2A, which is composed almost entirely of Red Phalaropes (com-

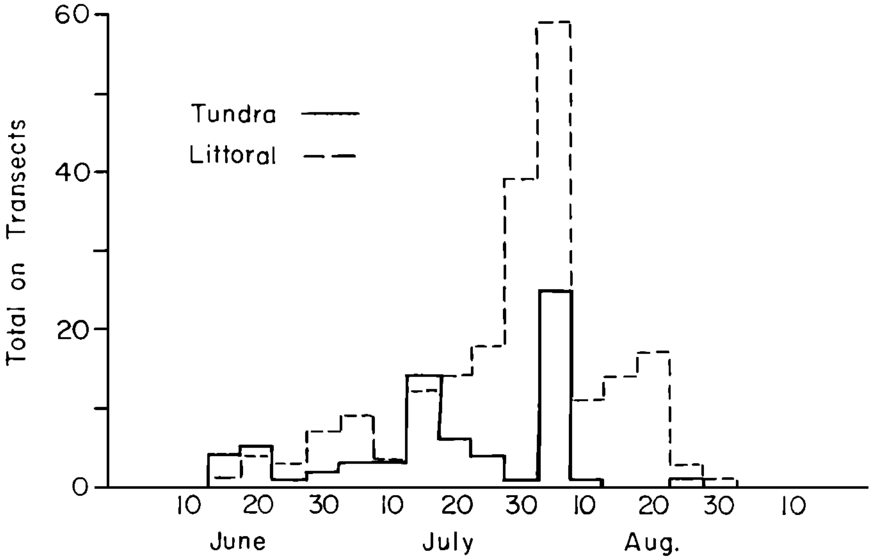

FIGURE 6. Seasonal habitat use, tundra vs. littoral, by Semipalmated Sandpipers.

pare Figs. 2A and 2B). The abrupt shift from tundra to littoral areas at the end of July includes a fairly heavy movement of migrating adult males, but the bulk of the shoreline phalarope activity consists of juveniles. Thus the difference in migration schedule between adult females, adult males, and juveniles accompanies pronounced differences in habitat use: Females seldom appear in littoral sites; males do so to an extent which changes with annual variation in the timing of sea-ice melt; and juveniles flood the littoral zone.

Ruddy Turnstones (Fig. 3C) display the same habitat use pattern in more modest proportions. After the young fledge, adults occur briefly in littoral areas, soon leaving the Barrow region. Throughout August and early September, juveniles are common on the beaches. Sanderlings, rare breeders near Barrow, occur in small numbers as spring migrants; in late summer, juveniles are common along gravel shorelines.

DISCUSSION

Assessing possible consequences of environmental disturbances requires two general classes of information concerning the nature of the physical disturbance and the ecological features of the area, especially the identity and characteristics of its species. The first of these depends upon collaboration between engineer, physical scientist, and biologist, because it entails not only the physical details of a particular development, but also its probability of occurrence, possible extent in geographic and habitat terms, and its time scale, as well as those of secondary effects. An excellent example of the desired level of collaboration is offered by Weller et al. (1978).

The second set of factors are more strictly biological. They rest upon four interacting considerations which must be established for each species:

1) Distribution. What species occur in the affected area; what is the nature of

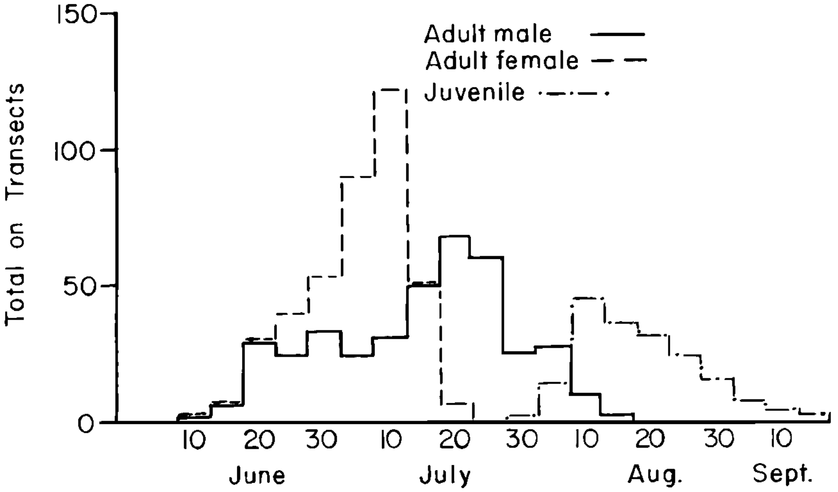

FIGURE 7. Seasonal use of tundra habitats by Red Phalaropes.

their activities (breeding, migration, etc.); how do population densities change seasonally and between years; is the area of critical importance for the local population; and how important is the area to the overall welfare of the species?

2) Habitat use. Different patterns of habitat use may render one species more susceptible than another by influencing its exposure to the disturbance. General differences in habitat preference (e.g. tundra vs. littoral) determine the probability of contact with the disturbance. For example, littoral zone habitats are more susceptible than tundra to damage from offshore oil spillage. Likewise, drainage patterns will determine the habitat effects of many tundra disturbances. On a finer scale, microhabitat differences will influence the severity of any effects arising from birds contacting spills within a general habitat type, as for example, the difference between shorebirds foraging above the water line vs. those wading or swimming.

3) Trophic relationships. The vulnerability of food resources to damage by development activities, as well as the dependence of a shorebird species on potentially affected food items and its ability to switch to other unaffected resources will influence sensitivity.

4) Social system and behavior. Differences in the seasonal occurrence and activities of different age and sex classes will set the schedule of exposure to any possible disturbance. Resulting population consequences will depend strongly upon which sex or age class is affected, and when the impact occurs during the reproductive cycle. Population dispersion patterns and individual spacing behaviors may also affect vulnerability to such events as oil spills, or the increase in predation caused by predator attraction to refuse sites. Under this heading also come a series of questions related to the effect of foraging behavior on exposure to different disturbances, and on responses to the disturbances themselves. For example, how tolerant are species of a particular disturbance, such as noise, during breeding or non-breeding activities?

Reviewing oil pollution impacts on bird populations in the North Atlantic,

TABLE 3
SHOREBIRDS POTENTIALLY AFFECTED BY OIL DEVELOPMENT NEAR BARROW, ALASKA

Coastal plain tundra		Littoral and offshore
Lowland	Upland	
Red Phalarope	Golden Plover	Red Phalarope
Pectoral Sandpiper	Ruddy Turnstone	Sanderling
Long-billed Dowitcher	Semipalmated Sandpiper	Ruddy Turnstone
?	Baird's Sandpiper	Semipalmated Sandpiper
?	Dunlin	Western Sandpiper
	?	Baird's Sandpiper
	?	Dunlin
		Long-billed Dowitcher
		?
		?

Bourne (1968) suggests that the most detectable consequences entail direct mortality from oil fouling, especially with waterfowl and seabirds. With the exception of phalaropes, the normal foraging behaviors of shorebirds reduce their immediate susceptibility to fouling relative to surface diving species. However, significant numbers of shorebirds of several species were found dead after spills in two estuaries in England in 1961 and 1966, presumably from direct toxic effects of oil. Compounding these direct actions, damage to habitat or prey populations is presumed to have been responsible for decreases ranging from 20% to 100% in several species' winter population sizes from one year to the next (Harrison 1967, Buck and Harrison 1967).

Our data on arctic coastal plain shorebirds allow preliminary estimates of the relative susceptibility of different species to effects of these kinds, in that they identify the species present, document their abundances, and describe general habitat use (Tables 3 and 4). They are tentative because they do not include all of the considerations listed above; our work continues to examine these issues and will refine the estimates. Table 3 lists the common shorebird species near Barrow, identifying those possibly affected by two general types of development, offshore vs. onshore. The question marks in the table indicate our uncertainty with respect to the type and magnitude of potential developments and their

TABLE 4
RELATIVE SUSCEPTIBILITY OF COMMON BARROW SHOREBIRDS TO LITTORAL ZONE DISTURBANCES

High	Moderate	Low
Red Phalarope	Semipalmated Sandpiper	Golden Plover
Sanderling	Western Sandpiper	Pectoral Sandpiper
Ruddy Turnstone	Baird's Sandpiper	
	Dunlin	
	Long-billed Dowitcher	

associated disturbances, as well as our need for more information on the biology of several of the less common species.

Table 4 estimates relative susceptibilities of the common Barrow shorebirds to disturbances in the littoral zone arising from outer continental shelf oil development. It is based primarily on the patterns reflected in Figure 2: the greater each species' relative use of littoral zone habitat, the more likely it is to be affected by such development. But we have also weighted our estimates with qualitative criteria based on population sizes and the magnitude of concentrations in littoral areas. The result is a somewhat subjective prediction of how likely a species is to suffer adversely from littoral zone oil-related activities in the Barrow area. As such they should provide a useful preliminary guide in management and planning decisions for coastal lowlands near Barrow.

ACKNOWLEDGMENTS

These studies were supported by the Bureau of Land Management and the National Oceanic and Atmospheric Administration as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP) and by the Energy Research and Development Administration (now Department of Energy). Carolyn Connors, Russell Greenberg and Frank Gress contributed greatly to the field effort. L. P. Myers helped in preparing the manuscript. We thank the Naval Arctic Research Laboratory (NARL) for logistic support.

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A PRELIMINARY ASSESSMENT OF TIMING AND MIGRATION OF SHOREBIRDS ALONG THE NORTHCENTRAL ALASKA PENINSULA

ROBERT GILL, JR.[1] AND PAUL D. JORGENSON[2]

ABSTRACT.—An intensive study of post-breeding and migrating shorebirds was conducted in 1976 on a major estuary of the Alaska Peninsula at Nelson Lagoon. Twenty species were recorded, eight of them breeding on the study area. Temporal patterns of relative abundance were obtained from aerial and ground censuses. Prominent events in the seasonal southward movements were (a) congregation of non- and post-breeding birds after mid-June, (b) an early migratory peak before early August dominated by Western Sandpipers, Short-billed Dowitchers, Least Sandpipers, and Whimbrels, and (c) a later, much larger peak in late Setember and early October dominated by Dunlins, Rock Sandpipers, Bar-tailed Godwits, and Long-billed Dowitchers. In the five-month period July–November, several hundred thousand shorebirds used the study area as a stopover and/or staging area. The most abundant species was the Dunlin. The area is also critical for such species as the Bar-tailed Godwit, apparently serving as a unique concentration site for this species prior to fall migration.

It is understandable that almost all Alaska shorebird investigations have concentrated on aspects of reproductive biology or other physiological processes while on the breeding grounds (for reviews, see, e.g., Holmes 1966a, 1966b, 1966c, 1971, 1972, Holmes and Pitelka, 1968, MacLean and Holmes, 1971, Norton 1972, Pitelka 1959 and Pitelka et al., 1974). Comparatively few Alaska studies have focused on post-breeding movements or staging patterns of migrant shorebirds. Indeed, over much of southwest Alaska and the Alaska Peninsula, an area with over 200 km^2 of intertidal substrates and 1800 km of coastline, there have been no studies directed specifically at migrant shorebird use of intertidal habitats. We know from cursory observations that over 30 species of shorebirds utilize these habitats during migration, often by the tens if not hundreds of thousands (Chapman 1904, Jaques 1930, Hurley 1931, 1932, Murie 1959, P. Arneson, M. Dick, D. Gibson, J. King, M. Peterson, unpublished data).

In this paper we report the results of the first quantitative assessment of the timing and migration of shorebirds along a major estuary of the north Alaska Peninsula.

STUDY AREA

The study was conducted along the northcentral Alaska Peninsula at Nelson Lagoon (56°00'N, 161°10'W) from 22 April through 1 December 1976 (Fig. 1). The north Alaska Peninsula is typified by a relatively regular coastline comprising numerous sand beaches, low terraces and alluvial fan deposits. The coastal lowland, which is dotted by numerous small lakes and drained by several river systems, extends inland between 10 and 20 km to the base of the Aleutian Range.

Nelson Lagoon is a 100 km^2 component of the larger 540 km^2 Herendeen Bay-Port Moller estuarine complex which, in itself, comprises approximately 44% of all estuarine habitat along the north Alaska Peninsula (P. Arneson, unpublished data). The Lagoon is fed by the combined discharge of the Caribou and Sapsuck rivers which originate in the Mt. Pavlof and Mt. Dana areas, respectively. The upper lagoon is a delta of several small, unstable islands grown to *Calamagrostis canadensis*, *Carex aquatilis* and *C. Lyngbyaei*. The adjacent uplands are grown predominantly to *Elymus arenarius mollis*, interspersed with *Honckenya peploides major* and *Lathyrus maritimus pubescens*. Several beds of *Zostera marina* occur throughout the estuary; however, none is present in Nelson Lagoon.

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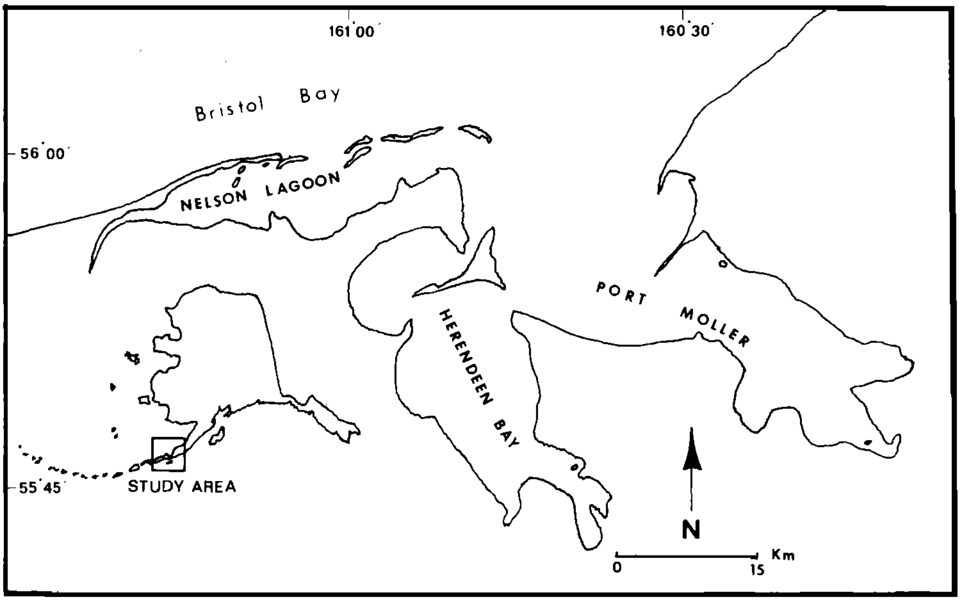

FIGURE 1. The study locale showing its position on the Alaska Peninsula.

The study was conducted over approximately 34 km² of western Nelson Lagoon (Fig. 2). Intertidal substrates within the study area were identified as: mudflats, 950 ha; mixed mud- and sandflats, 3250 ha; and rocky beaches, 300 ha. Barrier islands (150 ha) and vegetated coastal sand dunes and beaches (280 ha) were used as high tide roosts by shorebirds. Approximately 575 ha of open water remains at MLLW (mean lower-low water).

The estuarine waters of the study area are usually ice free between late April and October. The weather during the study was quite variable. May, July and September mean minimum and maximum temperatures were recorded as 2–7°, 9–13°, and 4–10°C, respectively. Prevailing winds are from the NW and SE during this period. The lagoon experiences two low and two high tides each lunar cycle and has a recorded mean diurnal tide range of 3.2 m.

METHODS

Shorebird data were derived primarily from aerial and ground censuses. Numerous incidental shorebird observations were collected during investigations of other components of the study area avifauna. An initial aerial survey of the study area was made by Gill on 23 April. A permanent field camp was established along Lagoon Point on 18 May, approximately 1 km E of the village of Nelson Lagoon. We were present on the study area between 18 May and 3 September, 13 September through 15 October and again between 17–24 November. Interim observations were provided by Mr. Peter Kust, Sr., who also acted as our pilot throughout the study.

Seven census areas were delineated within the study area and their intertidal substrates identified and mapped (Fig. 2). Census areas ranged between 56 and 950 ha.

GROUND CENSUSES

Between 21 May and 16 September, ground shorebird surveys focused on census area II, in front of our study headquarters. Censuses were conducted approximately every four days using a 20× spotting scope. We counted all birds on the area but made no distinction among species use of substrate types. A second type of census, also conducted approximately every four days throughout this same period, was directed specifically at shorebirds and their substrate selection. Several additional ground censuses were conducted on census areas I and III–VII but were conducted too infrequently to evaluate patterns of occurrence and abundance. The chief value of these surveys was to

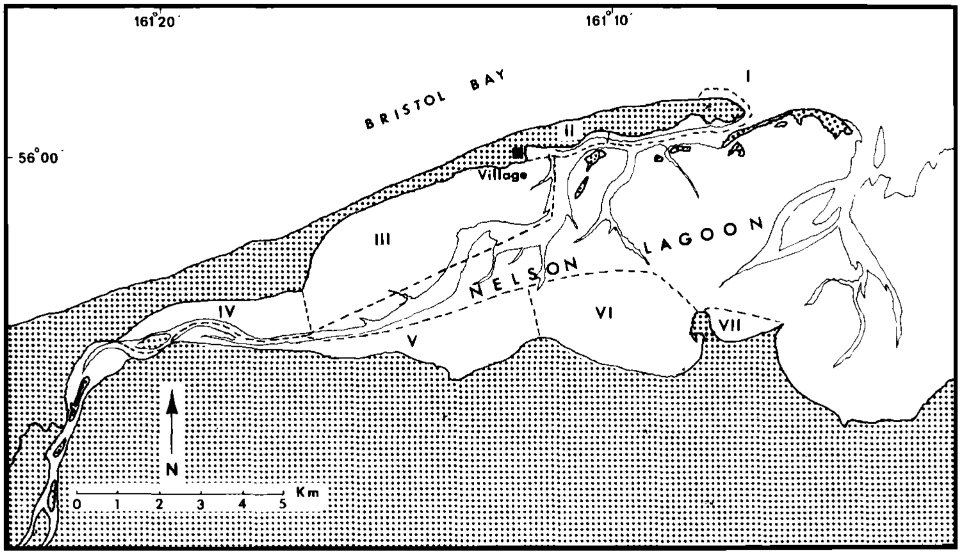

FIGURE 2. The Nelson Lagoon study area showing shorebird census areas I–VII.

provide comparative data for aerial and ground censuses over the same area during the same tidal cycle.

Aerial Censuses

Between 1 July and 15 October, weekly aerial surveys were flown over census areas I–VII. Only one census was conducted over area I during July. No censuses were flown over any of the areas between 3–13 September. From 16 October through 1 December, bi-weekly censuses were flown over all areas.

Censuses were flown in a Piper Super Cub at an elevation of between 50 and 75 m and at an airspeed of 75 knots. The pilot plus one observer conducted most censuses. Only the observer counted shorebirds but often relied on the pilot to locate concentrations of birds. Of 16 total censuses, Gill conducted 10, Jorgensen 4, while Kust flew 2 during our absence in October and November. Censuses were flown 1.5 hours before or after low, slack tide. Census duration averaged 45 minutes. Censuses started at area I and followed in sequence through area VII.

Shorebird numbers were voice recorded on magnetic tape and later transcribed to census forms. Censuses were conducted by first flying the edge of the substrate/water interface since most shorebirds were found concentrated along this area during early stages of each low tide. We then returned to survey other portions of each census areas as we saw shorebird concentrations. The airplane invariably disrupted concentrations of foraging shorebirds; however, we found most concentrations resettled within several hundred meters of their initial area. We feel duplicate counts from any one area or between areas were, therefore, at a minimum. During most of the study, shorebirds were recorded in groups of 100's except during peak migration in September and early October when we often counted shorebirds in groups of 1000's.

Shorebirds were usually identified to species except during late June through August when populations of Western Sandpipers (*Calidris mauri*), Dunlins (*C. alpina*) and Least Sandpipers (*C. minutilla*) occurred together over much of the study area. For purposes of this study these species were recorded as "small sandpipers" during censuses. Populations of each were subsequently determined from periodic comparisons of population ratios of all three species. These were derived from ground censuses conducted usually within 72 hours of an aerial census. Only ground and aerial censuses conducted over the same area or similar substrate types were used for such comparisons. We found numbers of *C. minutilla*, however, to be too small and the species' occurrence too irregular to accurately evaluate use patterns for each census area.

Numbers of Short-billed (*Limnodromus griseus*) and Long-billed Dowitchers (*L. scolopaceus*) were

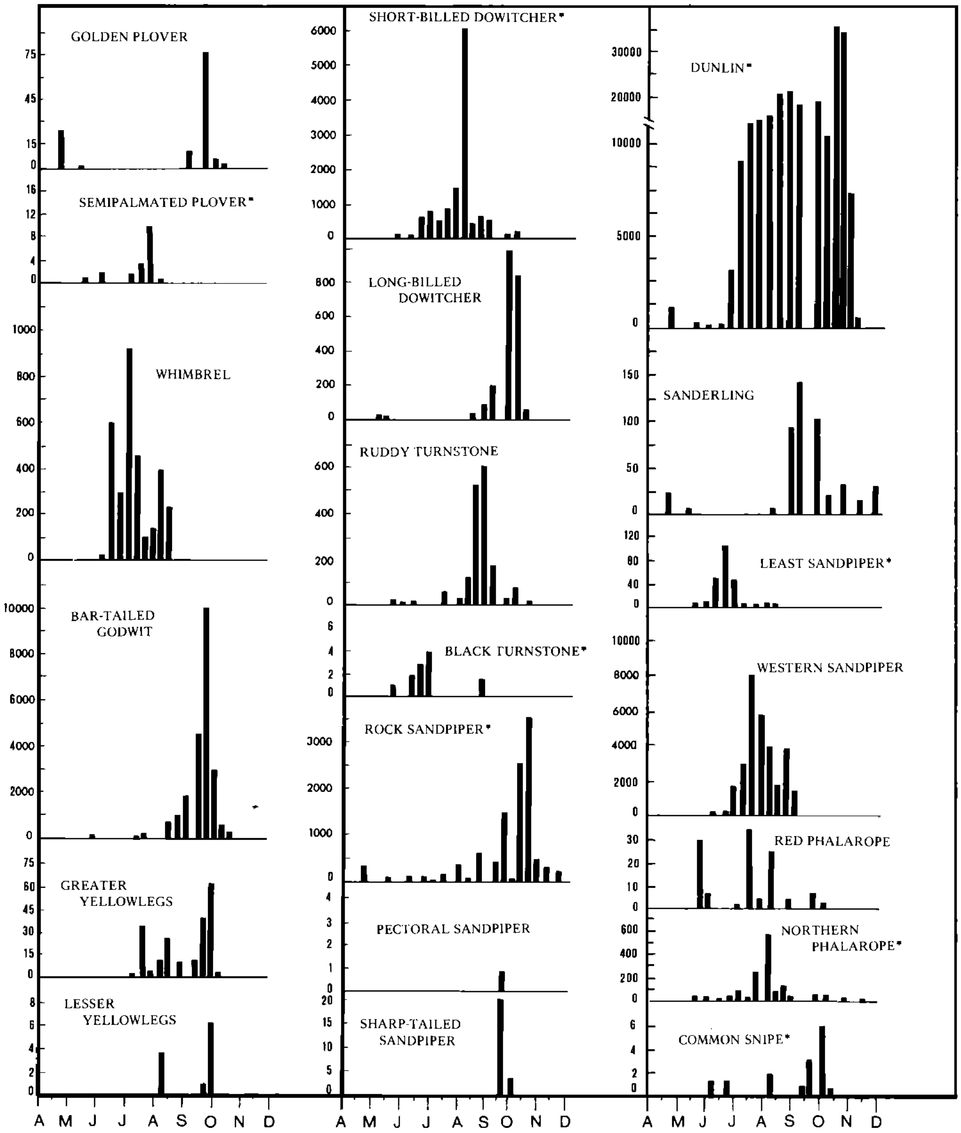

FIGURE 3. Comparative temporal abundance of 20 shorebird species at Nelson Lagoon, 22 April–1 December 1976. Species histograms incorporate aerial as well as ground census data obtained prior to migratory buildups beginning in late June. Numbers prior to 1 July do not necessarily reflect overall shorebird use of the study area but do accurately reflect timing of migratory buildups. Species noted by an asterisk nested on the study area.

similarily derived but presented less of a problem since the two species exhibited different habitat preferences and only briefly overlapped in occurrence during the study.

RESULTS

OCCURRENCE

Twenty species of shorebirds were recorded during the study, eight of which nested locally (Fig. 3). Of the nesting species, only Northern Phalaropes (*Lobipes*

TABLE 1

Amount and Composition of Substrate Types within Each Census Area, Nelson Lagoon, Alaska, 1 July–1 December 1976

	Census area							
Substrate type	I	II	III	IV	V	VI	VII	Total
Sand dunes and beaches	40[a](100.0%)[b]							40 (1.0%)[c]
Rocky intertidal beaches	6 (35.0)	4 (24.0)	6 (35.0)				1 (6.0)	17 (0.5)
Mudflats			101 (16.0)	486 (75.0)	40 (6.0)	18 (3.0)		645 (19.0)
Mixed mud and sandflats	10 (0.5)	53 (2.0)	830 (30.5)		769 (28.0)	930 (34.0)	130 (5.0)	2722 (79.5)
Total	56 (1.5%)[d]	57 (1.5)	937 (27.0)	486 (14.0)	809 (24.0)	948 (28.0)	131 (4.0)	3424 (100.0)

[a] Amounts are in hectares.
[b] % of all such substrate within the study area.
[c] % composition of total study area.
[d] % by census area of total study area.

TABLE 2
PERCENT SHOREBIRD COMPOSITION BY SUBSTRATE TYPE FROM 16 AERIAL CENSUSES, 1 JULY–1 DECEMBER 1976, NELSON LAGOON, ALASKA

	Habitat type				
	Sand dunes and beaches	Rocky intertidal beaches	Mudflats	Mixed mud/sandflats	Open water
Species					
Northern Phalarope					100.0%
Short-billed Dowitcher			0.8%	3.0%	
Long-billed Dowitcher			2.5	1.0	
Rock Sandpiper		72.0%		<0.5	
Dunlin	84.5%		75.1	80.0	
Western Sandpiper	15.5		20.7	9.7	
Bar-tailed Godwit				4.9	
Sanderling				<0.5	
Greater Yellowlegs			1.0	<0.5	
Lesser Yellowlegs			<0.5	<0.5	
Whimbrel				<0.5	
Golden Plover				<0.5	
Ruddy Turnstone		28.0		<0.5	
Total nos. recorded	52,500	4000	10,000	260,000	130
Percent of total	16.0	1.0	3.0	80.0	0.1

lobatus), Rock Sandpipers (*C. ptilocnemis*), Least Sandpipers and Dunlin nested in significant numbers, probably fewer than several hundred pairs each.

Since we did not open a permanent field camp until 18 May, early spring occurrence data are incomplete. During the aerial survey of Nelson Lagoon and Port Moller on 22 April, much of the intertidal area was still ice fast. Nevertheless, small numbers of Golden Plovers (*Pluvialis dominica*), Sanderlings (*C. alba*), Dunlins and Rock Sandpipers were present along ice free intertidal areas. We detected small numbers of Golden Plovers, Bar-tailed Godwits (*Limosa lapponica*), Red Phalaropes (*Phalaropus fulicarius*) and Dunlins moving northeast along the Peninsula through early June. Beginning mid-June, populations of post- and non-breeding shorebirds began congregating on the study area. We found that once a migrant species settled onto the area it remained at various population levels until fall departure. Populations of Dunlins, Ruddy Turnstones (*Arenaria interpres*), Red and Northern phalaropes and Short-billed Dowitchers remained for approximately 100 days. Golden Plover, Greater Yellowlegs (*Tringa melanoleucus*), Lesser Yellowlegs (*T. flavipes*), Black Turnstone (*A. melanocephala*), and Long-billed Dowitchers were present for less than 70 days during autumn migration, while Pectoral (*C. melanotos*) and Sharp-tailed Sandpipers (*C. acuminata*) were present for less than 30 continuous days.

Most species departed by the second week of October just prior to a major storm system which passed over the southwest Peninsula. Rock Sandpipers and Sanderlings were both present on the study area on 22 November as were Red and Northern phalaropes. The former two species are considered winter residents of the Alaska Peninsula and Aleutian Islands (Gabrielson and Lincoln 1959). Neither phalarope has been reported in the Bristol Bay area after the first week of November, but we do not consider our late November sightings unusual since much of Alaska experienced an abnormally mild fall and winter during 1976–1977.

TABLE 3

TOTAL SHOREBIRDS AND THEIR DISTRIBUTION RECORDED FROM AERIAL CENSUSES, 1 JULY–1 DECEMBER 1976, NELSON LAGOON, ALASKA

	Total nos. recorded	Census area						
		I	II	III	IV	V	VI	VII
Species								
Northern Phalarope	130	77.0%						23.0%
Short-billed Dowitcher	8600	0.5	23.0%	45.0%	0.5%	2.5%	2.5%	26.0
Long-billed Dowitcher	2500		23.0	23.0	7.0	28.0	5.0	14.0
Rock Sandpiper	4000	25.0	47.0	27.0				0.5
Dunlin	260,000	20.0	10.0	54.0	1.5	5.0	7.0	2.5
Western Sandpiper	36,000	24.0	21.0	34.0	1.5	6.0	9.5	4.0
Bar-tailed Godwit	13,000			87.0		1.0	12.0	<0.5
Sanderling	400			97.0		3.0		
Greater Yellowlegs	130				32.0	48.0	20.0	
Lesser Yellowlegs	6				33.0		67.0	
Whimbrel	1000					15.0	28.0	57.0
Golden Plover	75			10.0		90.0		
Ruddy Turnstone	1000	85.0	6.0	4.0		<0.5	0.5	4.5
Total numbers	326,000	62,500[a]	38,000	169,500	4700	16,500	24,000	11,000
Percent of total		19.0	12.0	52.0	1.5	5.0	7.0	3.5

[a] Predominantly roosting birds.

HABITAT UTILIZATION

Table I breaks down the various substrate types within each area by size and composition. A mixture of fine sand and mud was the predominant intertidal substrate and it occurred over all but census area IV. This area encompassed the delta region of the Caribou and Sapsuck rivers. As such, the substrate was a mixture of fine silt and organic materials. Census area I, Lagoon Point, was comprised mostly of barrier sand dunes and sand and rock beaches. During August and early September this area was used as a high tide roost by virtually all Dunlins and Western Sandpipers within the study area. Counts of both species returning to roost at Lagoon Point on 8 and 18 August and 2 September were only 6, 4, and 12% higher, respectively, than aerial counts of all "small sandpipers" taken within 48 hours of the same dates over census areas I–VII.

We did not find shorebird selection of Lagoon substrates to vary appreciably from previously reported habitat preferences for each species (Table 2). Rock Sandpipers and Ruddy Turnstones were most frequently observed along rocky intertidal beaches while few were observed on mud/sandflats. Both Greater and Lesser yellowlegs preferred mudflats and to a lesser extent mud/sandflats. We did not, however, record either species on area III which accounts for 16% of the mudflat substrate in the study area and which lies immediately adjacent to the extensive mudflats in area IV. Three species, Dunlin, Western Sandpiper and Short-billed Dowitcher utilized portions of mud/sandflats within all census areas. Golden Plovers, Bar-tailed Godwits, Sanderlings, and Whimbrels (*Numenius phaeopus*), were only found on mixed sand/mud substrate. Whimbrels, however, were never recorded on area III, which accounts for 30% of this substrate type within the study area. Long-billed Dowitchers tended to prefer mudflats, especially along the upper reaches of the Lagoon, while Short-billed Dowitchers

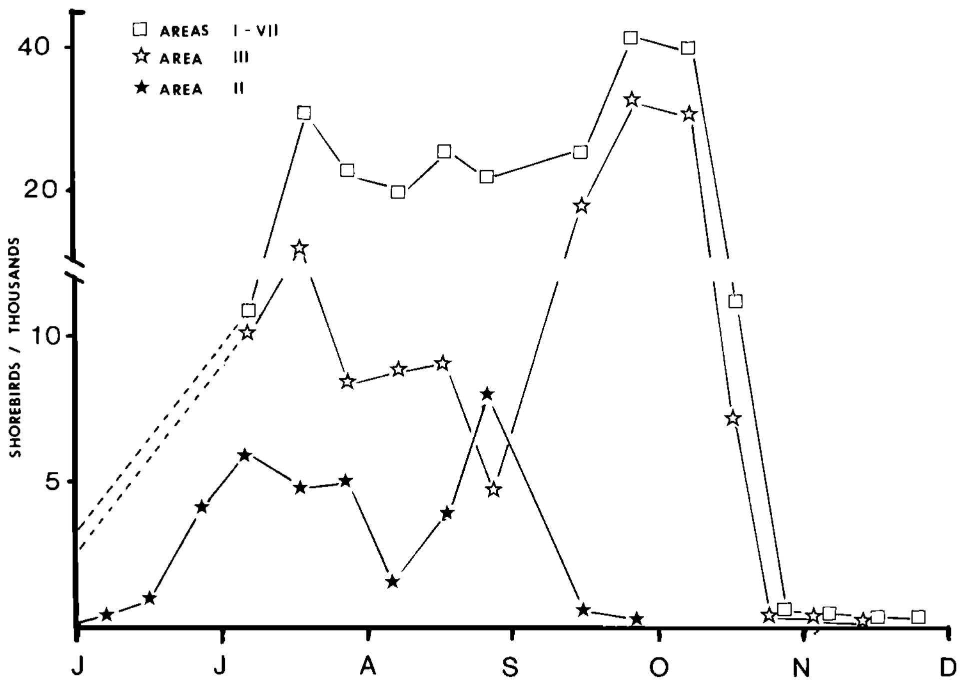

FIGURE 4. Peak periods of migration and approximate total numbers of shorebirrds on the census areas (squares), on census area III (open stars) and on census area II (closed stars). Census area II incorporates ground census data prior to 1 July.

were most frequently observed on mud/sand substrate. This difference in substrate selection between the two species has also been observed on their wintering grounds (Lenna 1969, Page 1975). Most of the shorebirds recorded on sand dunes and beaches were roosting.

ABUNDANCE

Table 3 presents percent shorebird composition in each census area as recorded during 16 aerial censuses. Total numbers reflect cumulative census results; since we did not qualify shorebird turnover, or determine ingress and egress to and from the study area, they do not represent overall numbers of shorebirds using Nelson Lagoon during autumn and fall migration. Comparative temporal abundance of all species is presented in Figure 3. These data incorporate aerial and ground census data obtained prior to migratory buildups beginning in late June. Numbers depicted prior to 1 July do not necessarily reflect overall shorebird use of the study area, but do accurately reflect timing of migratory buildup.

Overall, total numbers increased steadily between late June and early October. Two peaks of migration were recorded during this period (Fig. 4). Western Sandpipers, Short-billed Dowitchers, Least Sandpipers and Whimbrels peaked between early June and early August. Whimbrels exhibited the earliest migration but it is unknown whether these birds represented non-breeders or unusually early autumn migrants. Isleib and Kessel (1973) report small numbers of nonbreeding Whimbrels as uncommon from late May through July on the Copper

River Delta (61° N). Fall migrant Whimbrels are reported to arrive on the Copper River Delta by late June and are common by mid-July (op. cit.).

A second, much larger, fall peak composed of Dunlins, Rock Sandpipers, Bar-tailed Godwits and Long-billed Dowitchers occurred between the last week of September and the first week of October. Twenty-seven percent of all shorebirds counted during the study were recorded during this period. This bimodal migratory movement was reflected on all census areas except area II, where shorebird use virtually ceased in late September just as fall numbers peaked over all other areas (Fig. 4). A possible explanation is over-exploitation of food resources, but we conducted no benthic studies to confirm this.

DISCUSSION

We found little comparative material concerning migratory chronology or abundance of fall migrant shorebirds along other coastal areas of the Alaska Peninsula. Robert Jones (pers. comm.) reports tens of thousands of Dunlins occurring each fall (1960–1973) on Izembek Lagoon, approximately 100 km W of Nelson Lagoon. More recently, Paul Arneson, Alaska Department of Fish and Game (pers. comm.), recorded 45,000 "small," 20,000 "medium" and 600 "large" shorebirds during a 13–16 October 1976 aerial survey of the north Alaska Peninsula between Ugashik and Izembek Lagoon.

Away from the Peninsula on Angyoyaravak and Hooper bays (61°N), Holmes (1971) found post-breeding Dunlins concentrating on tidal flats in late July, and by late August he reported tens of thousands along several miles of coastline. Although he made no September observations, Holmes felt, based on the timing of arrival on wintering areas, that Dunlins remained through most of the month.

At Nanvak Bay (59°N) along the northwest corner of Bristol Bay, M. Dick and M. Petersen (unpublished data) found comparatively little fall Dunlin use of mudflats in 1971 and 1973. Between July and September 1976, Petersen observed Dunlins on Nanvak Bay on only four occasions. Other species using this area, including Whimbrel, Least and Rock sandpipers, Ruddy Turnstone, and Greater Yellowlegs had similar fall occurrence patterns as those found at Nelson Lagoon (M. Dick and M. Petersen, pers. comm.).

We also found that the occurrence of these species at Nelson Lagoon coincided with fall movements of the same species through Prince William Sound and the North Gulf of Alaska (60°N) (Isleib and Kessel 1973). However, the period of peak fall migration of Western Sandpipers and Dunlins through Prince William Sound has been recorded as much as 30 days ahead of Nelson Lagoon and both species are reported to occasionally overfly the Sound in fall (S. Senner and P. Isleib, pers. comm.).

These fragmentary occurrence patterns corroborate the suggestions of Holmes (1966) and Holmes and MacLean (1971) that the fall migration from staging to wintering areas of Dunlins is direct and rapid. Furthermore, the large concentrations of Dunlins along the Alaska Peninsula, the comparatively later staging period at Nelson Lagoon and elsewhere along the Peninsula, and the lack of such reported concentrations along coastal south and southeast Alaska during this period, allow us to hypothesize that Dunlins (*C. a. pacifica,* see Holmes and MacLean 1971) staging on Nelson Lagoon embark for their winter quarters on a direct transoceanic migration of the northeast Pacific. It seems unlikely that Dunlins coming from northern breeding grounds on the Yukon-Kuskokwim Delta, and staging along the western Alaska Peninsula, would move northeast again to Prince William Sound before continuing south along or off the coast of British Columbia. Dunlins reported from Prince William Sound in fall are probably flying directly from the Yukon-Kuskokwim breeding grounds, while an additional segment of this population moves south across Bristol Bay to Nelson Lagoon and other estuaries along the western Peninsula. We hope to confirm this by extensive banding and color marking in 1977.

The heretofore unreported large numbers of Bar-tailed Godwits observed on Nelson Lagoon in 1976 and the absence of such concentrations from elsewhere in Alaska suggests that Nelson Lagoon is probably the major fall staging area for most of the Alaska breeding population and not Nunivak and areas farther north as Gabrielson and Lincoln (1959) suggest. Confirmation of this will require observations during subsequent seasons.

ACKNOWLEDGMENTS

We thank the villagers of Nelson Lagoon for allowing us to conduct this study over much of their lands and for their hospitality and support throughout the study. We especially thank Peter Kust, Sr., our pilot, for making available his airplane, piloting skills and knowledge of the study area. Anthony DeGange, U.S. Fish and Wildlife Service, assisted in much of the field work and provided helpful comments on earlier drafts of the manuscript. Gerry Sanger and Jim Bartonek are also thanked for their critical reviews of the manuscript.

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MIGRATORY SHOREBIRD POPULATIONS ON THE COPPER RIVER DELTA AND EASTERN PRINCE WILLIAM SOUND, ALASKA

M. E. "PETE" ISLEIB[1]

ABSTRACT.—The spectacular concentrations of shorebirds moving north through the Copper River Delta and eastern Prince William Sound areas of southern Alaska are described. These are critical staging areas for a number of long-distance migrants and take on special interest now for conservation and environmental agencies with the development of a major oil terminal at nearby Valdez. It is estimated that this sector of the Alaskan coast is host to 20 million shorebirds each spring, the bulk of them being Western Sandpipers and Dunlins. The fall migration is not striking, being spread out over more time and over a greater diversity and quantity of habitat suitable for shorebirds.

The major portion of Nearctic shorebirds breeding in western Alaska utilize a narrow coastal migration corridor while en route north from their wintering grounds. Shorebird species that utilize this route are found wintering from southern Alaska to Terra del Fuego. Most shorebirds migrating north to the arctic and subarctic by way of the western slope of North America are confronted with a combination of topographic and climatic restrictions when entering the Pacific Northwest coast of British Columbia and southeastern Alaska. Snow-covered and glaciated mountain ranges rise abruptly from the sea, leaving little or no tidelands and marshes suitable for feeding and resting shorebirds. In addition, during the months of April and May, the region is still exposed to an easterly movement of frequent cyclonic storms. Thus, shorebird migrations are often hampered.

As birds progress north, the open sweep of the Pacific Ocean ends abruptly near 60 degrees north latitude in the northern rim of the Gulf of Alaska. Many shorebirds entering into this region have traveled in excess of 1500 km since encountering an abundance of good foraging habitats. Many of these birds have to travel another 1000 km or more to breeding habitats. The additional distance, at times over mountain ranges, will include overland flights of hundreds of kilometers.

Migrant shorebirds entering coastal central southern Alaska are confronted with two notable topographic obstacles: the St. Elias, Chugach and Kenai contiguous mountain ranges in a northern arc bending from the southeast to the southwest; and beyond these, the Alaskan and Aleutian ranges. These ranges contain the highest mountains and largest ice fields and glaciers in North America. During early May, most land and freshwater areas are under a mantle of lingering snow and ice.

On the periphery of the northern Gulf of Alaska, two areas offer the majority of suitable resting, feeding, and staging habitats in the form of shallow estuaries, fertile tide flats and marshes. The Copper River Delta and contiguous areas on Orca Inlet and Controller Bay contain over 1000 square kilometers of habitats intensively used by shorebirds. Three hundred kilometers to the west, Lower Cook Inlet offers hundreds of square kilometers of habitats in Kachemak and Kamishak bays.

This restriction of habitats to a few locations accounts for spectacular concen-

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trations of shorebirds during a brief period in the spring. Spring migrant shorebird concentrations are further enhanced by the fact that the duration of the shorebird migration is telescoped at this northern latitude. The main passage of migrants occurs during a two-week period and the entire migration period is less than five weeks.

For the past fourteen years, I have been active afield in the Copper River Delta-Prince William Sound area during the period of shorebird passage and specifically engaged in migration monitoring activities during the past six years. In the course of these years, I have observed and in some cases tried to census spectacular aggregations of shorebirds. I have identified 36 species of North American shorebirds and recorded 23 as regular and occurring in noticeable volumes.

On the Copper River Delta, the arrival of the "snipes," as they are referred to by the area's clam diggers and fishermen, are synonymous with spring. This is so much so that should a warm, balmy day occur during the third week in April, just prior to the arrival of shorebirds, clam diggers and fishermen are concerned to the point of calling me on the radio and asking, "What's happened to all them snipes?" At times I have had a hard time convincing some of the interested fishermen that the birds were not all wiped out by an oil spill somewhere in the south.

On or about 25 April, the first migrant shorebirds arrive on the Copper River Delta. With the first rush of arriving shorebirds, during the last week in April, almost all regularly occurring species have been recorded. During the 14-year period, 1963 through 1976, four years stand out as being unusual—1964, 1967, 1971, and 1973. During these years phenomenal masses totaling a million or even millions of shorebirds congregated on parts of the western Copper River Delta and in contiguous Orca Inlet. The sum of 250,000 to 500,000 shorebirds at one time utilizing approximately 50 square kilometers of tidal flats in southern Orca Inlet during one day within the first ten days of May is considered a normal and expected volume.

The second year that I was present in the area was 1964 and the year of the Alaskan earthquake which uplifted the delta landmass by two meters. On 16 May 1964 (an exceptionally late date for high numbers) I observed a large foraging mass of birds east of Copper Sands on the western Copper River Delta. After three hours of strip and block censusing, I calculated approximately 250,000 shorebirds (mainly Western Sandpipers, *Calidris mauri*) in a 2.5 square kilometer area of tidal flats. This location was part of a 40 square kilometer area of tidal flats and the entire area contained large numbers of shorebirds. At that time I estimated the total area may have contained 1½ to 2 million birds.

In early May 1967, in the Mummy Island area of southern Orca Inlet, I observed another concentration of shorebirds similar to the 1964 phenomenon. While I made no attempt to census, I roughly estimated the area contained several 100,000's and guessed after viewing nearby tidal flats that the entire southern Orca Inlet hosted well over a million shorebirds.

While conducting aerial waterbird surveys of Prince William Sound in May 1971 another exceptionally large volume of Western Sandpipers and Dunlins (*Calidris alpina*) was observed on the tide flats of Orca Inlet, near the city of Cordova. At that time, the personnel of the Special Studies Office, U.S. Fish and Wildlife Service, and myself participating in the Prince William Sound aerial surveys, could not come up with a practical, unhazardous and accurate method of censusing these shorebird volumes from aircraft. We tried at low tide, but were spooked by the wheeling masses of birds at too close quarters to the aircraft. At the next high tide a large percentage of these birds had departed the area. The 1971 aerial waterbird surveys of Prince William Sound also placed me in a position to observe a variety of shoreline and open-water habitats during the peak of spring shorebird migrations. During these surveys, I observed on one occasion a single raft of at least 50,000 Northern Phalaropes (*Lobipes lobatus*) in Hinchinbrook Entrance, Prince William Sound (right in the middle of what is now the oil tanker route, into and out of the Valdez terminus of the Trans Alaska Oil Pipeline). We also noted 10,000's of staging Surfbirds (*Aphriza virgata*) and estimated the Ruddy Turnstone (*Arenaria interpres*) population exceeded 100,000 on island beaches in the sound. The shores of Montague Island, were host to large numbers of American Golden and Black-bellied plovers (*Pluvialis dominca* and *P. squatarola*), probably 20,000 to 25,000 combined. Since we also observed Bristle-thighed Curlew (*Numenius tahitiensis*) during these surveys, we considered it probable that at least some of the plovers and turnstones may have been arriving in the area via long distance overflights of the North Pacific from islands in the central Pacific.

In 1973, extra large masses of shorebirds occurred in Orca Inlet. In that year, I made daily counts of shorebirds utilizing 15 square kilometers of tidal beaches and flats between Hartney Bay and the boat harbor in the city of Cordova. Daily strip and block censuses were made shortly after half tide on the flood from 28 April through 31 May. The numbers of shorebirds utilizing the censused tide flats exceeded 2 million between 6 May and 10 May. During the 34 days of observed passage, frequent changes in species composition gave the impression of a rapid migrational turnover. Based on an estimate of total migrational turnover of birds every three tidal ranges, the censused area was host to at least 11 million "peeps" between 28 April and 31 May. Of this total, the bulk of the passage included Western Sandpipers (6½ million) and Dunlins (3½ million). Approximately one million other small shorebirds included some interesting counts—a flock of over 100,000 Least Sandpipers (*Calidris minutilla*) and flocks of up to 10,000 Sanderlings (*Calidris alba*). Additionally, in excess of one million medium and large shorebirds were censused on these tide flats. These included large numbers of Long-billed and Short-billed dowitchers (*Limnodromus scolopaceus* and *L. griseus*), Surfbirds, Red Knots (*Calidris canutus*) and turnstones (*Arenaria* sp.).

For the past three years (1974 through 1976), the U.S. Fish and Wildlife Service has conducted stationary point migration watch studies near Mummy Island in southern Orca Inlet. This location is within a natural topographic funnel that is extensively used by coastal migrant birds. During the peak of migration, tens of thousands of birds pass hourly in view of the migration watch location. The migration watch study consists, in part, of 15-minute indexes from each daylight hour (04:00 through 22:00) of all migrant bird species crossing a north/south line. Items recorded are species (or most definitive grouping category), number, direction of flight, elevation, point of crossing, and time. Also recorded are the weather conditions, stage of tide, and visibility. Now of considerable volume, hourly indices of data are presently being prepared for statistical treatment by

Michael Jacobson, U.S. Fish and Wildlife Service, Special Studies Office, Anchorage, Alaska. This study is programmed to be continued in 1977.

Some 5 km south of the migration watch location, along the beaches of the outer coast, a light but steady westward movement of shorebirds (mainly Western Sandpipers) occurs throughout the daylight hours in May. The migration watch location near Mummy Island is at the Copper River Delta-Orca Inlet interface and receives a steady exchange of migrating and staging birds going both east and west. The movements to the east represent staging birds forced by tidal action to high tide resting and loitering areas on Egg Island on the Copper River Delta and shorebirds that overflew the area during the night and are returning to foraging areas on the delta. The majority of the shorebirds appear to migrate long distances at night. On numerous occasions we have observed shorebirds departing the Copper River Delta and Orca Inlet almost en masse. At these times, usually at sunset or late in the evening twilight, scores of flocks numbering up to several hundred birds each will lift off the tidal flats and climb to high elevations (observed up to 1000 m) and head west.

An interesting bit of data we have gathered is the current volume of Red Knots utilizing the Copper River Delta as a staging area each spring. During the mid-1960's, I estimated the area was the principal staging zone for about 10,000 Red Knots. During the late 1960's and early 1970's that number was upgraded to approximately 40,000 to 50,000. In the last two years, this number has been refigured from new data and we now estimate the area hosts a staging population of about 100,000. Single flocks of 7000 to 10,000 have been recorded regularly in the past three years and one flock was estimated at 40,000, more Red Knots than I had earlier thought were in the Pacific Coast migration corridor.

The absolute number of migrant shorebirds utilizing the coastal habitats along the northern rim of the Gulf of Alaska is unknown. However, based upon my 14 years in the Copper River Delta-Orca Inlet area and an additional 3 years in the Cook Inlet area, I have roughly estimated that the entire coastal region is host to something in the range of 20 million shorebirds each spring.

The Copper River Delta-Prince William Sound region is annually host to a large percentage of these birds. During May 1976, Alaska Department of Fish and Game personnel reported a mass of 1 to 2 million shorebirds (some 80% Western Sandpipers) located on the tidal flats at the head of Kachemak Bay in lower Cook Inlet (Paul Arneson, ADF&G pers. comm.).

Fall shorebird migrations in south-coastal Alaska are diffused over the period from the third week in June through October and dispersed over additional habitats that are not available (due to ice and snow coverings) during the spring. Extensive, but not intensive, habitat utilization by southbound migrant shorebirds occurs in south-coastal Alaska. Aggregations of shorebirds exceeding ten's of thousands have not been recorded. Available data suggest that a large percentage of southbound migrant shorebirds stage nearer their breeding grounds in northern or western Alaska and overfly or bypass the northern coasts of the Gulf of Alaska.

In conclusion, the general awareness of the magnitude of shorebird populations utilizing a few locations in south-coastal Alaska is new. Some of these data were first mentioned in print only a few years ago (Isleib and Kessel, Univ. Alaska Biol. Paper 14:1–149, 1973). These data were responsible for continued interest and studies in shorebird migration phenomena in the south-coastal Alaska region;

and they are the primary basis for the State of Alaska administration's proposal of a bill to the state legislature to create the "Copper River Delta Critical Habitat Area." The principal criterion for this 1000-plus square kilometer zone of special designation is the intensive utilization by migrant waterbirds, especially shorebirds. This designation will prioritize these wildlife habitats for waterbirds above alternate uses.

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AN EVALUATION OF THE COPPER RIVER DELTA AS CRITICAL HABITAT FOR MIGRATING SHOREBIRDS

STANLEY E. SENNER[1]

ABSTRACT.—The migration strategies of the northwest Pacific Coast populations of the Dunlin and Western Sandpiper are compared with reference to their use of the Copper-Bering River deltas in the northern Gulf of Alaska as a stopover and staging area in spring. Dunlin arrive with depleted fat reserves and use the area to replenish these not only to fuel migration to breeding grounds, but to provide energy for the initiation of reproductive activity. Migrating Western Sandpipers show less variation in weight along the Pacific Coast, and no significant gain in mean weight occurs across the delta system. This suggests less within-population coordination of migratory movement and/or shorter flight range than is seen in the Dunlin, but at the level of the individual, the delta system is critical for replenishment of fat reserves for migration and reproduction in the Western Sandpiper, also. It appears that the completion of the annual cycle in these two and probably other shorebird populations depends significantly on access to and use of the Copper–Bering River delta system during spring migration.

Each year in April and May, more than 20 million waterfowl and shorebirds pass through the Copper River Delta in south-central Alaska. Species which are trans-Gulf or trans-Pacific migrants may make their first landfall in Alaska in this area (Isleib and Kessel 1973). More than half of these 20 million migrants are either Dunlins (*Calidris alpina pacifica*) or Western Sandpipers (*Calidris mauri*). For both species, the Copper River Delta is a stopping point for great percentages of their respective breeding populations (Isleib and Kessel 1973).

Collectively, the Copper and Bering River deltas (hereafter referred to as the C-BRD system) constitute an isolated break or habitat island in this north Pacific region otherwise dominated by steep fjord-like coastal topography with limited intertidal habitats. The Copper River alone, with 1/6 the discharge, transports ¼ the sediment and a greater amount of sand than the Mississippi River (Galloway 1976). The vast sandy and muddy intertidal zone (about 500 km^2) and associated supratidal wetlands of the C-BRD system attract an assemblage of migrating and breeding birds distinct from those of the heavily forested, steep, and rocky coastal areas stretching almost uninterrupted from the Puget Sound and southern British Columbia to Bristol Bay and the Yukon-Kuskokwim Delta in western Alaska. Contributing to the C-BRD system's intriguing qualities are its relatively wide tidal range (about 3.5 m at Cordova) and long history of seismic activity (Committee on the Alaska Earthquake 1971).

Because ice and snow cover much of the supratidal wetlands in late April and May, migrant shorebirds are largely obligate users of the intertidal zone, though some feeding and loafing occurs at the thawing margins of freshwater ponds. In May, densities up to 250,000 shorebirds per $mile^2$ of mudflats have been recorded in Orca Inlet at the western fringe of the Copper River Delta (Isleib and Kessel 1973). Isleib describes the phenomenon of migration elsewhere in this volume.

Within the tidal flats the shorebirds follow a typical and well described behavioral pattern (e.g., Holmes 1966, Recher 1966). The shorebirds feed with both the rising and falling tides; the most intensive activity is associated with the receding

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tide line. At high tides dense aggregations of loafing birds form above high tide line. Aerial displays among mixed-species flocks are frequent.

Petroleum- and natural gas-related activities in the Prince William Sound and northern Gulf of Alaska will include oil tanker traffic to and from Valdez (scheduled to begin in mid-1977) and the exploration and possible development of outer continental shelf lease tracts in the northern Gulf. One lease sale has been held in the northeastern Gulf, and a second is scheduled. Additionally, a natural gas liquifaction and tanker facility is proposed for Point Gravina, about 25 km northwest of Cordova. If this facility is constructed there will be a large thermal discharge into the Sound's cold waters, with unknown consequences for intertidal and marine organisms (F. P. C. Staff 1976).

There is no doubt that oil will be spilled in the region as a result of these petroleum-related activities, and that some of it will come ashore (USDI 1976). When and in what amounts oil will be spilled, and with what ultimate destinations, are unanswered questions.

In view of the several energy-related developments in store for Prince William Sound and the northern Gulf, can the C-BRD system be considered a critical habitat in the annual cycle of Dunlins, Western Sandpipers, and possibly other shorebird species? My purpose in this paper is to establish the significance of the C-BRD system to shorebirds by considering 1) the vulnerability of their food resources with respect to oil spills, and 2) the energy reserves of individuals in migration along the Pacific Coast and within the C-BRD system. Some of the results presented here are from research in progress. However, considering the developments described above it is timely to present our current state of knowledge with respect to the potential relationship between oil and shorebirds in the C-BRD system.

STUDY AREAS

The physiography and climate of the northern Gulf of Alaska and Prince William Sound region, including the intertidal zone, have been described by Rosenberg (1972) and Isleib and Kessel (1973). The Copper and Bering River deltas—the C-BRD system—are prominent features of this region. The present study focused on tidal flats at 3 sites within the system: Controller Bay, the mouth of the Eyak River, and Hartney Bay in Orca Inlet (Fig. 1).

Controller Bay is a sheltered indentation in the Gulf of Alaska coast. At low tides much of Controller Bay is a flat plain of mud and sand. Martin (1908) described the Controller Bay region in considerable detail. Activity in the present study focused on the eastern shore of the low-lying Kanak Island and the Bering River Delta.

The second study site was located on the plain between the intertidal portions of the Eyak River and Government Slough to the east of the Eyak River. At low tides this triangle-shaped, silty plain is part of the Copper River flats extending across the mouth of the Copper River west into Orca Inlet (Galloway 1976). The Copper River Delta was uplifted an average of 1.89 m by the 1964 earthquake (Reimnitz and Marshall 1965) and the upper portion of what was formerly intertidal zone is now a sedge (*Carex* spp.) flat. Above this "old" intertidal zone is a region of wetlands and marshes extending inland, in some cases as far as 13 km, to the base of the Chugach Mountains (Isleib and Kessel 1973). The plant communities of the wetlands consist primarily of sedges, grasses, and some shrubs (Potyondy et al. 1975).

Orca Inlet, including Hartney Bay, the third study site, represents a transition into the fjord-type environment of Prince William Sound. Orca Inlet is bordered by the rocky shore typical of Prince William Sound, yet it is very shallow because of sediments transported westward from the Copper River. At low tides much of Orca Inlet is an exposed mud and sand flat. Hartney Bay itself is nested against the west side of the Heney Mountain Range where it is sheltered from the prevailing southeasterly winds. Several freshwater streams feed into Hartney Bay, and again because of earthquake

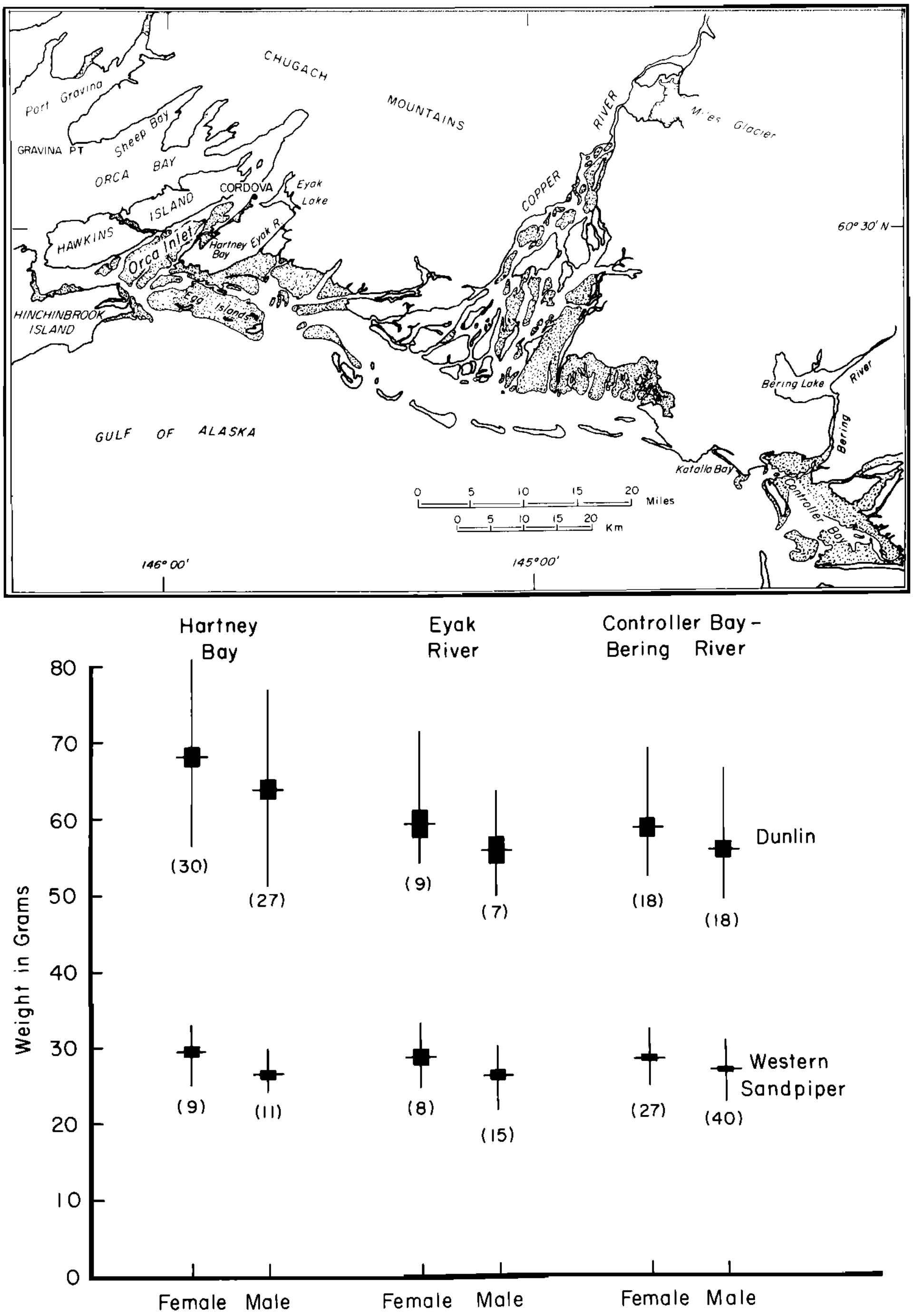

FIGURE 1. Map (top) showing Copper-Bering River delta system and study sites. Stippled areas are tidal flats. Weights (bottom) of *Calidris alpina* and *Caldris mauri* collected concurrently at three locations in the C-BRD system. The horizontal line is the mean, the solid rectangle is the standard error of the mean, and the vertical line is the range. Sample sizes are in parentheses.

uplift, there is an extensive sedge zone between the present high tide line and the "pre-earthquake" rocky shore. A road crosses the flats at the northeastern end of the bay.

Tides in the region are semi-diurnal, with a marked inequalty between successive low waters (Rosenberg 1972). During the study period, 30 April to 27 May 1976, the mean tidal range was about 3 m at Cordova. Weather data are gathered at the Cordova FAA station on the Copper River Delta. During the study period the average maximum and minimum temperatures were, respectively, 9.3°C and 1.2°C, with a mean of 5.2°C. Precipitation totaled 17.9 cm (NOAA 1976).

BREEDING AND WINTERING RANGES

The prime breeding range for Western Sandpipers and Dunlins in western Alaska is the Yukon-Kuskokwim Delta and the Seward Peninsula (AOU 1957). Western Sandpipers, less commonly, nest as far north as Barrow and as far east as Camden Bay (Holmes 1972). The Dunlins nesting abundantly at Barrow are *C. alpina sakhalina*, a subspecies which migrates and winters along the Pacific Coast of Asia (MacLean and Holmes 1971, Norton 1971). *C. alpina pacifica* (the Dunlins referred to throughout this paper unless otherwise indicated) nest only as far north as Cape Thompson (MacLean and Holmes 1971), while they winter from the northern Gulf of Alaska to Baja California (AOU 1957, Isleib and Kessel 1973). Western Sandpipers winter along the Pacific Coast from California to Peru and along the southern Atlantic Coast and the Gulf of Mexico, south to Central America and northern South America (AOU 1957).

PHENOLOGY OF SPRING MIGRATION

Spring migration in California begins in late March and April for Western Sandpipers and Dunlins, respectively, and ends in early May for both species (Jurek 1973). Many Dunlins apparently shift from a coastal to an interior route during spring migration in California (Page 1974). Peak numbers of *alpina* in interior western Oregon were reported between mid-March and mid-April (Strauch 1967). At Cultus Bay, Puget Sound, Van Zelzen (1973) reported the largest numbers of *alpina* in March and April and peak numbers of *mauri* in mid-May. Richardson (in Van Zelzen 1973), at the northern end of Vancouver Island, found that *mauri* were abundant as early as 23 April and peaked in the first week in May. At the same location *alpina* were first recorded on 28 April. In the Vancouver area in 1970, large numbers of *mauri* passed through from 26 April to 15 May (Campbell et al. 1972).

Holmes (1966) suggested that Dunlins move north to British Columbia and then fly directly across the Gulf of Alaska to Alaska. Munro and Cowan (1947) classify *alpina* as abundant transients along the British Columbia coast, while *mauri* are considered common. Both species are common at Glacier Bay National Monument, Alaska, according to Wik and Streveler (1967).

During the second and third weeks in May, Dunlins and Western Sandpipers combined outnumber all other shorebird species on the Copper River Delta (Isleib and Kessel 1973). So far as is known, virtually all Dunlins of the *pacifica* subspecies pass through the C-BRD system in spring. Western Sandpipers migrating through the C-BRD system include most of their entire population, though at least a small number migrate through interior continental United States (Parmelee et al. 1969).

Little is known about migration between the C-BRD system and the Yukon-Kuskokwim Delta. On 11 May 1976, 1 to 2 million "small" sandpipers, an estimated 80% of which were *mauri*, were sighted on the Fox River flats at the head of Kachemak Bay in lower Cook Inlet (D. Erikson, unpubl. data). Arrival dates in the Yukon-Kuskokwim Delta reported by both Conover (1926) and Holmes (1971, 1972) for *mauri* and *alpina* were between 10 and 20 May, inclusive.

TABLE 1
ORIGINS OF WEIGHT RECORDS

Location	Record type[a]	Species *C. mauri*	 *C. alpina*
San Quintin Bay	S	Museum Vert. Zoology	Museum Vert. Zoology
Salton Sea	S	San Diego Mus. Nat. Hist.	San Diego Mus. Nat. Hist.
San Francisco Bay	S	Museum Vert. Zoology	Holmes 1966
Bolinas Lagoon	C	Point Reyes Bird Obs.	Point Reyes Bird Obs.
Humboldt Bay	C	R. Gerstenberg, unpubl. data	Gerstenberg 1972
Puget Sound	C	—	S. Shanewise, unpubl. data
Vancouver Island	C	Brit. Columb. Prov. Mus.	Brit. Columb. Prov. Mus.
Controller Bay	S	This study	This study
Eyak River	S	This study	This study
Hartney Bay	S	This study	This study
Hooper Bay	S	R. Holmes, unpubl. data	R. Holmes, unpubl. data
Cape Thompson	S	Museum Vert. Zoology	—

[a] Key to symbols: S, collected specimen; C, live-captured bird.

METHODS

Between 30 April and 27 May 1976, *alpina* and *mauri* specimens were collected, while they were feeding, at the 3 sites in the C-BRD system. The shorebirds were collected at various times of day, stages of the tide, and levels within the intertidal habitat. Two transects were established normal to the tide line at Hartney Bay to provide a basis for collecting the shorebird specimens and sampling invertebrate prey species in the mudflats. We weighed shorebird specimens to the nearest 0.5 g in the field using Pesola spring balances. Their stomach contents were removed and placed in buffered formalin as soon as possible after collection. Carcasses were frozen, and all samples were transported to the University of Alaska, Fairbanks, for analysis.

In Fairbanks the stomach contents have been sorted, their key parts counted, and the whole items weighed. Data analysis, however, is not yet complete. Dr. George West, Institute of Arctic Biology, University of Alaska, is presently determining lipid levels in the bird carcasses (the technique is described in West and Meng 1968).

Whole body weights of *alpina* and *mauri* specimens from museum collections, the literature, and unpublished records of various investigators were assembled to provide a perspective from which to view the weights of specimens secured in the C-BRD system. Table 1 shows the sources for weight data by species and location. Because the specimens from a given site were often collected on widely scattered dates, it was necessary to lump these data into 2 broad categories. The first interval, 2 March–15 April, roughly corresponds to the first half of spring migration (depending on the specific site), while the second 16 April–31 May, corresponds to the latter half of migration and early breeding (at Hooper Bay). Mean body weights are reported only for those sites and intervals for which I found at least 5 specimen records.

Potential flight ranges were estimated for a sample ($N = 10$ for each species, with equal sex ratios) of specimens on which lipid extractions are complete. The formula developed by McNeil and Cadieux (1972) was used.

RESULTS

Most prey taken by Western Sandpipers and Dunlins (Tables 2 and 3) in the C-BRD system are intertidal invertebrates. Note that several species of bivalve molluscs are preyed on by both *mauri* and *alpina*. A small sample of both shorebird species from Hartney Bay in May 1975, showed that many molluscs, and amphipods, also, were taken (Senner 1976).

Dunlins of both sexes show substantial weight gains when comparing the mean body weights from samples at either Controller Bay or the Eyak River to Hartney

TABLE 2
STOMACH CONTENTS OF *Calidris mauri* AND *Calidris alpina*[a]

Items	*Calidris mauri* A[b]	*Calidris mauri* B[b]	*Calidris alpina* A	*Calidris alpina* B
Pelecypoda				
Macoma balthica	60	4.1	95	27.9
Mytilus edulis	40	2.7	13	13.0
Mya spp.	20	24.0	13	1.0
Astarte spp.	6	1.0	—	—
Unidentified	6	2.0	—	—
Copepoda				
Harpacticoida	20	13.7	—	—
Amphipoda				
Corophium spp.	—	—	4	1.0
Unidentified	6	1.0	23	+
Insecta				
Diptera	6	1.0	—	—
Chironomidae	47	48.7	4	1.0
Acarina				
Unidentified	6	1.0	—	—
Animal				
Unidentified frag.	6	2.0	4	1.0
Plant				
Unidentified seeds	27	3.5	9	21.5
Unidentified debris	73	+	54	+
Grit				
<1 mm	60	299.2	90	10.7
≥ 1 mm	60	43.3	23	7.6

[a] For *C. mauri*, $N = 15$; for *C. alpina*, $N = 22$; collected while feeding on the Hartney mudflats, May 1976.

[b] A = frequency (percent of stomachs with item), B = average number of items per stomach. Items which could not be quantified are indicated by "+".

Bay (Fig. 1). Female *alpina*, for example, show a 16.2 percent gain in mean weight when comparing the samples from Hartney and Controller Bays. Male and female *mauri*, on the other hand, show nearly constant mean weights across the C-BRD system (Fig. 1).

During migration along the Pacific Coast Dunlin females show a general increase in mean body weight (Fig. 2). Male *alpina* have a similar pattern, though they average several grams lighter. Western Sandpiper males show a small but significant ($P < 0.05$) increase in mean weights between the two intervals at Humboldt Bay (Fig. 3). With the exception of the Vancouver Island sample, however, the mean weights remain relatively constant when compared to those of the Dunlins. The pattern for females is similar, though they average several grams heavier. Individual *mauri* weights range from 17 to 35 g in males and up to 42 g (at Bolinas Lagoon) in females. The respective coefficients of variation for *mauri* males vary from 2.79 to 13.28 percent, while those for *alpina* females vary from 1.73 to 14.05 percent.

Comparing the mean fat indices (g fat/g fat-free dry weight) for *mauri* and

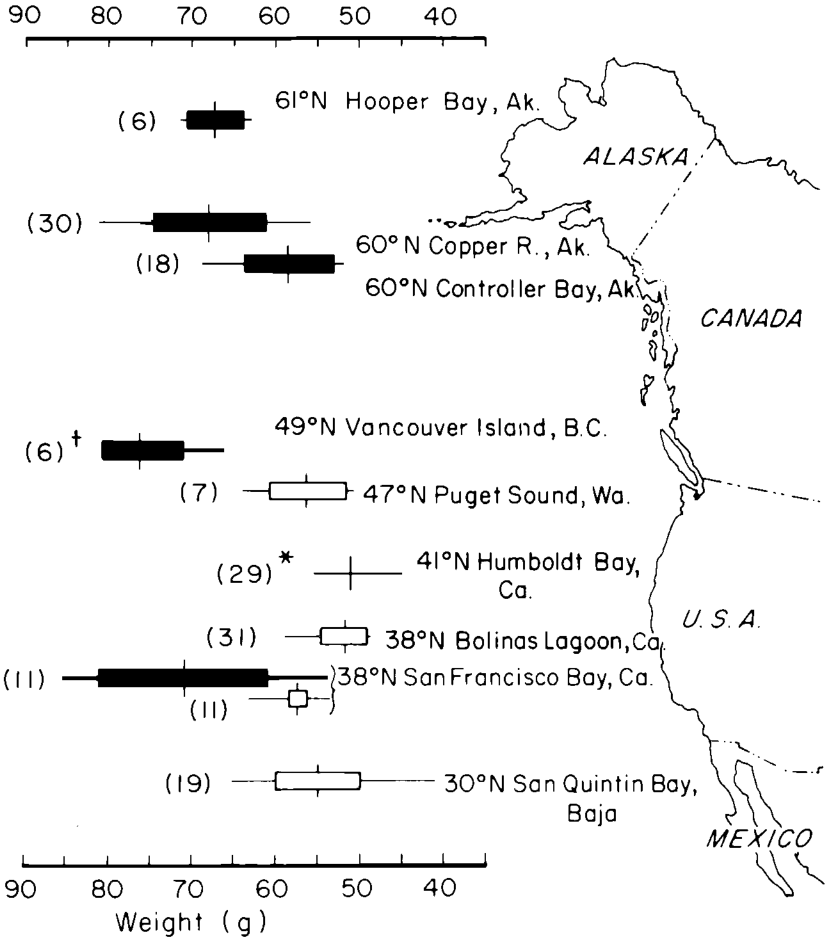

FIGURE 2. Weights of female *Calidris alpina* during spring migration along the Pacific Coast. The vertical line is the mean, the rectangle is the standard deviation, and the horizontal line is the range. Open rectangles indicate samples from 2 March to 15 April, and dark rectangles indicate samples from 16 April to 31 May. Sample sizes are in parentheses. ★ Unable to calculate standard deviation from this source. The sample is from the earlier interval. + The upper limit of the range = 79.5 g.

alpina at Hartney Bay shows that *alpina* are significantly fatter than *mauri* (0.46 ± 0.03, $N = 17$, and 0.17 ± 0.02, $N = 18$, respectively; $P < 0.05$) as they leave the C-BRD system. These different fat levels are reflected in the shorebirds' estimated flight range capabilities (Fig. 4). Western Sandpipers have about half the mean estimated range of Dunlin: 600 ± 77 km (R = 177–1081) compared to 1260 ± 89 km (R = 744–1791).

DISCUSSION

Food Resources

Interpreting the contents of stomach samples is difficult because of differing digestion rates for different types of prey items (e.g., molluscs vs. polychaetes)

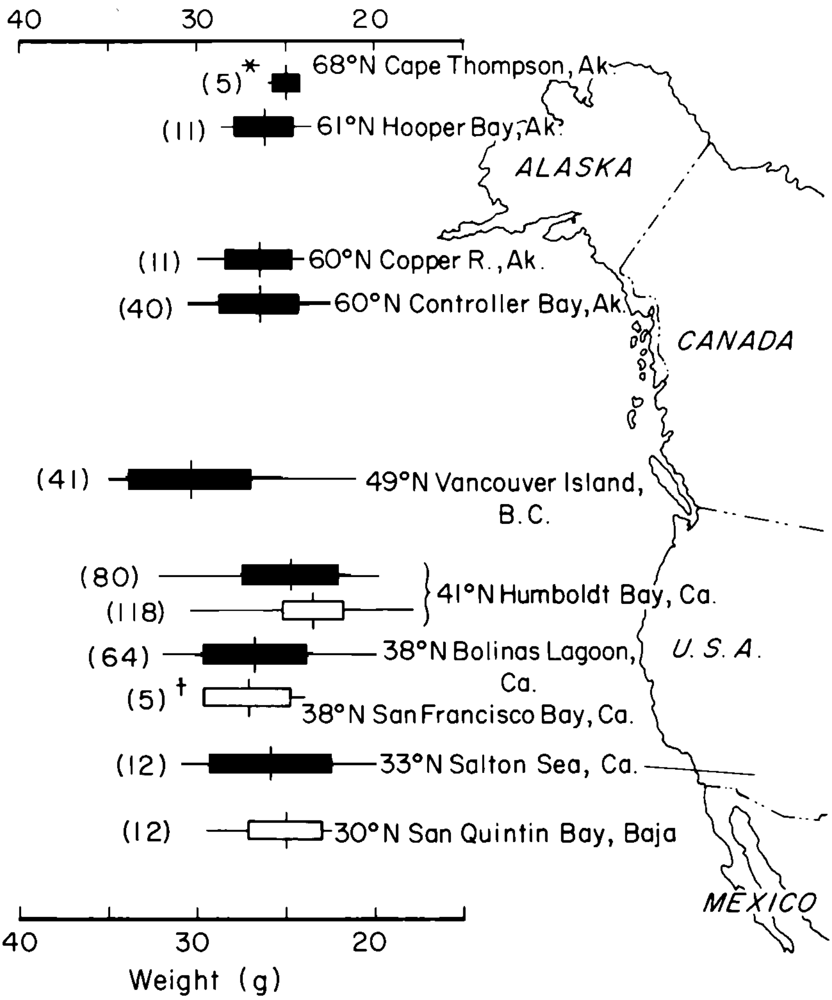

FIGURE 3. Weights of male *Calidris mauri* during spring migration along the Pacific Coast. The symbols are the same as in Fig.2. + The upper limit of the range = 29.0 g. ⋆ The lower limit of the range = 24.3 g.

(e.g., Goss-Custard and Jones 1976). There is no doubt here, however, that both *mauri* and *alpina*, but especially *alpina*, are preying on many bivalve molluscs. *Macoma balthica*, by far the most frequently taken mollusc (Tables 2 and 3), is an abundant pelecypod with a circum-arctic distribution (Coan, 1971). It is a frequent prey of many shorebird species (e.g., Wolff 1969, Goss-Custard and Jones 1976). My own sampling of *M. balthica* showed densities up to about 2600 per m^2 on the Hartney Bay mudflats, and Myren (in press and pers. comm.) has recorded densities up to 3200 per m^2 (not including individuals able to pass through a screen with square openings 3.2 mm per side) in the Dayville mudflats at Port Valdez.

Shaw et al. (1976) suggested that *M. balthica* has good potential as an "indicator" of oil pollution in sediment habitats. He simulated stranding of an oil slick

TABLE 3
STOMACH CONTENTS OF *Calidris mauri*[a]

Items	A[b]	B[b]
Nematoda		
Unidentified	5	1.0
Pelecypoda		
Macoma balthica	60	7.6
Mytilus edulis	5	1.0
Mya spp.	20	1.8
Insecta		
Diptera	55	3.7
Chironomidae	65	8.1
Tipulidae	5	1.0
Staphylinidae	5	1.0
Plants		
Unidentified seeds	25	1.8
Unidentified debris	55	+
Grit		
<1 mm	100	186.6
≥ 1 mm	100	40.5

[a] N = 20, collected while feeding on the mudflats at the mouth of the Eyak River, May 1976.

[b] A = frequency (percent of stomachs with item); B = average number of items per stomach. Items which could not be quantified are indicated by "+".

on a mudflat at Valdez Arm and found that mortality in a naturally occurring *M. balthica* population increased significantly with increasing duration of exposure. Laboratory studies by Taylor et al. (1976) showed *M. balthica* responded to the presence of oil by coming to the sediment surface, a response which would, in a natural environment, make them susceptible to tidal action, exposure (freezing and desiccation), and predation.

Studies elsewhere have considered the effects of accidental oil spills on invertebrate life. Oil may smother, foul, or directly poison intertidal organisms. Single spills may be relatively short-term in their effects, while chronic pollution is more likely to have long-term effects (Boesch et al. 1974, Crapp et al. 1971). Given the petroleum-related developments projected for the northern Gulf of Alaska, it is not unreasonable to conclude that the intertidal invertebrates of the C-BRD system are in a vulnerable position.

In light of the shorebirds' dependence on vulnerable intertidal organisms, how will the shorebirds be affected if their food resources should greatly diminish in availability and/or quality? I have approached this question by examining the energy reserves of *alpina* and *mauri* as they move through the C-BRD system.

ENERGY RESERVES

Fat is the primary source of energy for birds in long-distance migratory flights (Odum et al. 1961), and birds making long migrations deposit fat before leaving the wintering grounds (Kendeigh et al. 1960; Nisbet et al. 1960). Fat deposits may also be replenished en route, since original reserves may be depleted before a final destination is reached (Odum et al. 1961). Hanson (1962) noted that Canada Geese (*Branta canadensis*) increase in body fat during their northbound migra-

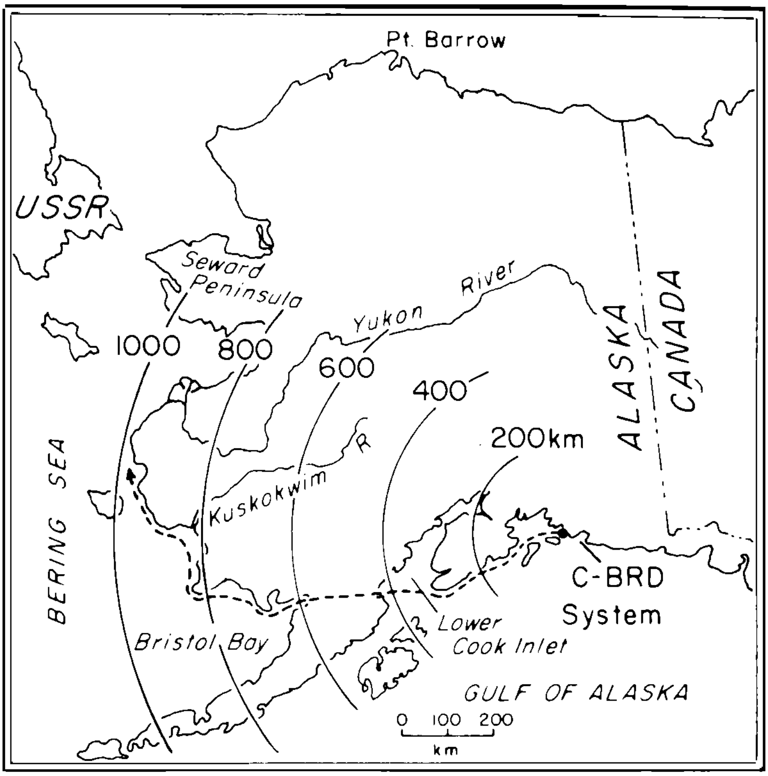

FIGURE 4. Flight distances from Hartney Bay in the C-BRD system to western Alaska. The dashed line shows a probable migratory pathway through lower Cook Inlet.

tion, and MacLean (1969) found that fat was used to support early season breeding activities in sandpipers in arctic Alaska.

Many investigators have reported the fat-free weight of a bird remains relatively constant while the lipid weight is highly variable; thus, changes in whole body weights reflect changes in fat reserves (e.g., Page and Middleton 1972). This generalization does not always hold (MacLean 1969), but in the present study lipid levels have been determined in enough specimens to show that whole weights do reflect fat reserves.

To best understand the weights recorded in the C-BRD system, it is useful to consider them in context with weights throughout spring migration.

Mean body weights in Dunlins increase during migration (Fig. 2). The fact that the mean of the Vancouver Island sample is the highest of the entire migration and that its range does not overlap with the range of the Puget Sound sample suggests two hypotheses. First, the absence of overlap with the range of the earlier Puget Sound sample suggests that individuals in Dunlin flocks migrate collectively (i.e., there is a communal response among members of a flock) rather than independently of each other (Recher 1966 contrasts the two approaches). Recher (1966) attributed a wave-like character to the migration of individual shorebird species in California, while Holmes (1966) noted that *alpina* populations at several locations in central California did not increase during spring migration.

He suggested the entire population shifted northward gradually in a slow-moving migration. Page (1974) pointed out that there are spring peaks for Dunlins at some locations in some years in coastal California and presented evidence that Dunlins shift to an inland rather than coastal route in spring migration in California.

Second, the high mean value at Vancouver Island compared to the much lower values at Controller Bay and the Eyak River is evidence supporting Holmes' (1966) suggestion that in spring Dunlins fly across the Gulf of Alaska from British Columbia to Alaska. Though *alpina* are reported along the British Columbia coast and at Glacier Bay (see "Phenology" section), so far as is known, there are no concentration points—spatially or temporally—between southern British Columbia and the C-BRD system which approach the magnitude of the C-BRD system.

Dunlins, then, at Controller Bay are light because they have depleted their fat reserves in making long, probably over-water flights. Since the mean body weights (Fig. 1) at the Eyak River site are essentially the same as the Controller Bay values (within the respective sexes), it is possible that arriving *alpina* first land at any number of sites across the C-BRD system.

Once within the system, however, *alpina* move from east to west, probably stopping repeatedly to feed as tides and weather permit. From field observations and comparisons of morphometric measurements such as culmen lengths (Senner, in progress), there is no evidence suggesting that distinct populations are making single stops in the C-BRD system and then leaving the region entirely. It is my impression that the richest feeding opportunities are at the western fringe of the system. For example, my limited sampling of intertidal organisms shows few *Macoma balthica* at the Eyak River site relative to the rich Hartney Bay mudflats. If the Orca Inlet area is the final staging/feeding opportunity before *alpina* depart on another flight to their breeding grounds in the Yukon-Kuskokwim Delta (and points north), then one would expect to find the heaviest birds there. This is indeed the case (Fig. 1).

It is not presently known what lengths of time transient shorebirds, including *alpina,* spend within the C-BRD system, though Isleib (pers. comm.) believes that at individual sites they may remain for only a few tide cycles. In terms of the rate at which fat can be deposited, it may be pertinent to note that juvenile *C. a. alpina* gained about 1 g (extreme of 3 g) daily after the third day in pauses in their autumnal migration in Sweden (Mascher 1966). Curlew Sandpipers (*C. ferruginea*) in Britain gained 2 to 4.5 g weight per day during pauses in their fall migration (Minton 1969). Lapland Longspurs (*Calcarius lapponicus alascensis*), in spring migration in the Yukon Territory, showed an average gain in fat of 0.76 g daily (West et al. 1968).

The pattern of weight change in Western Sandpipers is much less clear than in Dunlins, but there are indications that the two species use different migratory strategies. Lumping the weights from a given site into extended intervals as was necessary here may obscure patterns which require a more sensitive approach. But it is conceivable that mean body weights for Western Sandpipers at a given site could remain relatively constant (Fig. 3) because the continuing influx and departure of individuals with different weights and thus, fat reserves, could balance each other out. If true, this suggests that individual *mauri,* to a greater extent than with *alpina,* migrate independently of each other (i.e., each pursues its own schedule), and that the flocks seen in migration may be relatively temporary and haphazard associations resulting from factors such as the limited availability of prime intertidal feeding habitats. West et al. (1968), West and Peyton (1972), and DeWolfe et al. (1973) document this migration pattern in three species of overland-migrating fringillids. One argument against the hypothesis of individual *mauri* pursuing their own schedules is that with this strategy one would expect much greater variability among the *mauri* at a given site when compared to the *alpina*. The similar coefficients of variation for the two species (see "Results") show this not to be true. Good series of birds captured or collected on a regular basis at specific sites would shed much light on the nature of the *mauri* migration.

Regardless of whether Western Sandpipers migrate as independent individuals or collectively, the fact that their mean body weight at Vancouver Island is the highest for any site (Fig. 3) again suggests a general readying for a demanding flight to Alaska. If not an over-water flight, it is at least a flight along a long, rocky coast with few extensive feeding opportunities. As was true with *alpina*, the *mauri* mean body weight at Controller Bay is substantially lower than the mean for the Vancouver Island sample.

Western Sandpipers show no gain in mean weights across the C-BRD system, nor are they as fat as Dunlin at Hartney Bay. A single non-stop flight from Hartney Bay to Bristol Bay should fully deplete the fat reserves for *mauri*, while *alpina* could fly well beyond that distance. It is misleading to assume, however, that the only value of fat reserves is to propel these birds to their breeding grounds. MacLean (1969) and Norton (1973) argue strongly that for calidridine sandpipers fat reserves play a critical role in the early phase of reproductive activity—a period of highest energy demands when weather conditions may reduce feeding opportunities. In Pectoral Sandpipers (*C. melanotos*), particularly, MacLean (1969) suggested breeding success is related to the fat reserves of individual males as they arrive in Barrow, Alaska, breeding grounds. Many arctic breeding species arrive on their breeding grounds with fat reserves that are not depleted until courtship, territorial activity, or egg-laying occur (Irving 1960).

In this context the observation of 1 to 2 million small shorebirds in lower Cook Inlet takes on new significance. It may well be that for *mauri*, particularly, intermediate stops between the C-BRD system and the Yukon-Kuskokwim Delta are a necessity. Note that the lower extreme of the *mauri* flight range (177 km) is not even sufficient to take them as far as lower Cook Inlet (Fig. 4). Comparisons of fat indices and estimated flight ranges for *mauri* and *alpina* could show that through the entire spring migration *mauri* tend to move in relatively short "hops" as opposed to long, sustained flights.

SUMMARY AND CONCLUSIONS

Migration Strategies

To contrast the migration strategies of Dunlin and Western Sandpipers, the former, as a population, shows weight gains as a result of fat deposition during spring migration. Dunlin may migrate collectively rather than as independent individuals. Dunlin appear to make long, over-water flights from southern British Columbia to Alaska and arrive in the C-BRD system with depleted fat reserves. The C-BRD system provides an opportunity to replenish depleted fat reserves not only to fuel migration to their breeding grounds, but to provide energy reserves for the early phase of reproductive activity.

Individual Western Sandpipers undoubtedly deposit and then use fat reserves during migration, but as a population they show less variation than Dunlins in mean body weights through spring migration. One possible explanation for these observations is that individual *mauri* migrate independently of each other. Western Sandpipers at Vancouver Island do show a gain in mean weight, indicating a readying for a strenuous flight to Alaska. The fact that their mean body weights do not change across the C-BRD system does not diminish the value of the system as a habitat in which individual *mauri* can replenish fat reserves needed for migration and reproduction. The shorter estimated flight range of *mauri* relative to *alpina* suggests a need for intermediate stops between the C-BRD system and the Yukon-Kuskokwim Delta. Further research is needed to determine whether a pattern of short hops typifies *mauri* migration in general.

Copper–Bering River Delta System

The C-BRD system is a unique habitat island in the northern Gulf of Alaska serving as a focal point in the spring migration of more than 20 million waterfowl and shorebirds. Oil- and natural gas-related developments in the northern Gulf region pose serious threats to intertidal invertebrate resources upon which many shorebirds depend.

Evidence is presented that the C-BRD system is a critical habitat in the annual cycle of the Dunlin and Western Sandpiper. If adequate feeding opportunities are denied them in the C-BRD system, it could seriously affect reproductive success in significant fractions of the entire populations of Western Sandpipers and the western Alaska subspecies of Dunlin.

The C-BRD system may be a critical habitat to shorebird species other than *mauri* and *alpina*. The Red Knot (*C. canutus*), for example, is a prime candidate, since a large portion of North America's Pacific Coast migrants apparently use the Copper River Delta's tidal flats during a brief interval in May (Isleib and Kessel 1973).

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RESULTS OF THE CALIFORNIA SHOREBIRD SURVEY

RONALD M. JUREK[1]

ABSTRACT.—A statewide shorebird survey program was conducted in California from July 1969 to June 1974. The objective of the program was to gather current data on the occurrence and abundance of shorebirds in selected wetland habitats throughout the state. California Department of Fish and Game established and coordinated the survey as part of its California Shorebird Study. Observers, mostly volunteers, counted shorebirds at established sites periodically during each year.

From one to five years of survey data were collected at 57 sites, and more than 2200 census reports were received. Computer tabulation of data was completed for the first three years of the survey. The data document the value of California's wetland habitats to shorebirds and provide baseline information for determining long-term population trends.

Wetlands in California support millions of migrating and resident shorebirds through the year. Economic development of these wetlands since the turn of the century has resulted in an alarming reduction in suitable shorebird habitat. By the mid-1960's, there was widespread concern for the future of shorebird habitats and populations in the state. This concern prompted an intensive statewide research program on shorebirds directed by California Department of Fish and Game. The need for this program was expressed in the Department's 1965 California Fish and Game Wildlife Plan.

Studies were initiated in July 1968. A six-member Shorebird Advisory Committee, composed of ornithologists, was appointed to provide technical assistance to this program. Members were Dr. Howard L. Cogswell, Dr. Mary M. Erickson, Dr. Stanley Harris, Dr. Joseph R. Jehl, Jr., Dr. L. Richard Mewaldt, and Dr. Frank A. Pitelka. The program was funded by the Federal Accelerated Research Program for Shore and Upland Migratory Game Birds and by Federal Aid in Wildlife Restoration, Project W54R.

The study was conducted in two major phases: a shorebird trapping, banding, and marking program and a shorebird survey and census program (Jurek 1973, 1974a). In addition, funding assistance was provided for several shorebird ecology studies (Gerstenberg 1972, Carrin 1973, Holmberg 1975), and an extensive literature review was compiled (Gerstenberg and Jurek 1972). The survey phase of this program, the California Shorebird Survey, is the subject of this paper. It consisted of a statewide network of census sites. The program was designed to provide current information on the occurrence and abundance of shorebird species in selected habitats in the state.

METHODS

In 1968–69, shorebird censusing methods were developed in studies at Point Reyes Peninsula (Sibley 1970), Humboldt Bay (Gerstenberg 1972) and San Diego Bay (Jehl and Craig 1971). Reporting forms and guidelines for census procedures were developed, and statewide censusing began in July 1969.

Sites were chosen in known shorebird concentration areas or in areas where information was needed on shorebird occurrence, abundance, species composition, and habitat use.

For each site, competent birders were recruited from local communities to volunteer their time and abilities as censusers. Participants were provided with basic survey instructions, specific site survey instructions, and reporting forms. Observers were also requested to search for and report color banded shorebirds which had been marked in the concurrent banding program.

Censusers conducted counts from established census routes or observation points at their sites.

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They scheduled counts at their convenience within the framework of their specific site instructions. They were requested to census at least twice each month. Counts were recorded on forms as to species abundance and habitat use. Also, weather and water conditions were recorded. The completed report forms were submitted to the department after each count. Reports received in the first three years of the survey were programmed for computer processing and tabulation.

RESULTS

More than 200 observers, mostly volunteers, participated in the survey program from 1969 to 1974. Their efforts yielded from one to five years of year-round count data at 57 sites, and more than 2200 census reports were received. Three or more years of data were collected at 28 of these sites. There were 21 inland and 36 coastal sites. Survey site descriptions and summaries of counts were reported by Jurek (1974b).

DISCUSSION

Shorebird species composition and abundance in a given area change frequently in response to seasonal migrations, tidal cycles, disturbances, restlessness in flocks, and many other factors that influence the daily movements of shorebirds. Shorebird census sites were too small and counts conducted too infrequently to adequately monitor these frequent population changes. However, the data provided useful information on habitat preference, relative abundance, distribution, and seasonal occurrence of species at selected sites over a wide area. This information has been incorporated into many reports in the Department of Fish and Game's Coastal Wetlands Series and in various environmental impact analyses. These data also provide a baseline for determining long-term populations trends. A recommendation resulting from the survey is that a similar statewide survey be initiated in 1978 in an attempt to assess long-term changes in shorebird populations in California.

The survey was subject to certain censusing problems, partly because of the variety of census sites and census conditions and the dependence on volunteer observers. Counts were not always conducted as regularly as requested or according to established procedures for the site. Also, censusers often experienced difficulties in identification of some species and in enumerating birds in large, mixed flocks. Despite some censusing problems, the performance of volunteer observers was outstanding. Many participated in three, four or all five years of the program. Without the volunteer assistance, the program would not have been possible.

By encouraging public participation, the survey program also stimulated local interest in shorebirds and helped focus public attention to the need for obtaining resource data on shorebirds and their habitats.

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CONSERVATION AND MANAGEMENT OF COASTAL WETLANDS IN CALIFORNIA

JOHN SPETH[1]

The title, "Conservation and Management of Coastal Wetlands in California," implies that you want to know what is being done to save the habitat for shorebirds, regardless of which agency or organization is involved in such preservation efforts. I am here to tell you about those efforts, of which I am aware, to preserve, maintain, and enhance coastal wetlands habitat. These efforts include activities of several state, federal, and local agencies and private organizations.

Time will not permit a detailed presentation of the various efforts—so, if you have a special interest in a particular wetland and you want to know what's happening there, I would be happy to discuss it with you after my presentation.

What do I mean when I way "coastal wetland"? Our definition in the Department of Fish and Game is all lands subject to regular or periodic tidal influence. We also include freshwater habitats in close proximity to the coast.

The Department of Fish and Game has what might be considered a two-part program to conserve coastal wetlands. The first is an information program to document the resource values of this critical habitat and to make this information available to decision makers as well as to interested publics. The second is an acquisition and management program. In order to tell you where we are toward attaining our goal of preserving and maintaining coastal wetlands, I want you to visualize a normal distribution curve: in my opinion the total government and private effort is about ¾ of the way up the curve. In noting progress on elements within the program, we are much further along on our information program than on our acquisition and management programs. In a sense, we've done a good job in identifying the problem. Now it's time to solve it. And we are beginning to do that.

At this point, before detailing some of the activities of the Department of Fish and Game and other agencies to conserve wetlands, I will digress for a moment and give you some background information on the overall status of coastal wetlands.

At the turn of the century, we estimated that the State of California possessed about 381,000 acres of *prime* coastal wetlands, more specifically, that area above low tide, including salt and brackish marshes and tide flats. During the ensuing 75 years, about ⅔ of this acreage was lost to a variety of developments which were thought to be of more value to man than maintenance of the marsh. We now have about 120,000 acres left. Much of the remaining acreage is owned and controlled by local agencies, including cities, counties, and harbor districts. These locally held wetlands were once owned by the state but subsequently granted to the local agencies by the legislature. There are some 180 parcels of land along California's coast which have been granted by the legislature to local government for their use, generally for harbor purposes. In addition to the locally controlled wetlands, a significant portion of the remaining wetlands are privately owned.

In 1968, when the department first began its program to preserve coastal wet-

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TABLE 1
PUBLICALLY OWNED COASTAL WETLANDS

Department of Fish and Game Owned Wetlands

Area	Acres	Cost
Buena Vista Lagoon	190	$ 750,000
Upper Newport Bay	700	3,400,000
Suisun Marsh	890	985,820
Pismo Lake	50	115,000
Tomales Bay	541	386,000
Heerdt Marsh (San Pablo Bay)	95	290,000
Total	2466	$5,926,820

Wetlands Leased by DFG from State Lands Commission

Area	Acres
Bair Island and Redwood Shores (SF Bay)	over 900
Coon Island (Napa Marshes)	250
San Pablo Bay Wildlife Area	10,000
Big Lagoon (Humboldt County)	1800 (incl. 350 acres marsh)
Bolsa Chica	560
Morro Bay (Exercise of Public Trust)	560
Total	14,070

Wetlands Owned by Other State or Federal Agencies

Area	Controlling Agency	Acres
Pescadero Marsh	(DPR, see below)	250
Los Penasquitos Lagoon	(DPR)	150
Tijuana River	(DPR & Navy)	150 (approx.)
Morro Bay	(DPR)	350 (approx.)
S. F. Bay NWR	(USFWS)	23,000[a]
San Pablo NWR	(USFWS)	11,711[a]
Humboldt Bay NWR	(USFWS)	8733[a]
Anaheim Bay NWR	(USFWS & Navy)	1100
Mugu Lagoon	(U. S. Navy)	1450
Elkhorn Slough	(Nature Conservancy)	500
Santa Margarita River	(U. S. Navy)	300
Goleta Slough	(Santa Barbara County)	360
Santa Ynez River	(U. S. Navy)	160
Bolinas Lagoon	(Marin County)	1240
Carpinteria Marsh	(University of California)	160

DPR = Department of Parks and Recreation
USFWS = U. S. Fish and Wildlife Service
NWR = National Wildlife Refuge

[a] Area within approved refuge boundary—only a small portion of this area has been acquired.

lands, we looked at areas in private ownership or under local control and predicted that by 1980 these lands would be largely developed and lost as wildlife habitat. Our Chief of the Wildlife Management Branch, at that time Ben Glading, had as a goal to save at least one area. The chosen area was Buena Vista Lagoon in San Diego County and now, 8 years and $750,000 later we own it. This, of course, is not the only coastal wetland that the department owns—I'll say more about our acquisition program later.

One of the most successful parts of our effort to conserve the state's coastal

TABLE 2
WETLANDS PROPOSED FOR ACQUISITION BY STATE AND FEDERAL AGENCIES

Area	Acres
Napa Marshes	10,000
San Elijo Lagoon	500
Batiquitos Lagoon	600
Ten Mile River	150
Lake Earl and Talawa	2200[a]
Elkhorn Slough	1400
Big River	150
Petaluma River	3000
Suisun Marsh	55,000[b]
Buena Vista Lagoon	7
Sweet Springs Marsh	25
Hanna Property (San Pablo Bay)	200
Suisun Bay	182
Various tidal channels and sloughs in South San Francisco Bay[c]	

[a] An undetermined acreage around the lakes is also planned for acquisition.
[b] Total acreage of marsh—only small portion to be acquired in foreseeable future.
[c] Acreage figure not available.

wetlands resource has been a series of published reports documenting the fish and wildlife values of these areas. To date, we have published 18 reports covering 20 separate coastal wetlands. In these reports we describe the habitat and the species of fish and wildlife found there; we describe the various types and degrees of people use of the resources; we identify existing and potential resource problems, such as planned developments; and last but not least, we make recommendations for preservation of the resource.

If you are interested in getting copies of these reports, they are available from the State Documents Section. I am strongly convinced that these reports have played a major role in the preservation of our remaining wetlands. Many of the policy statements in the state's coastal plan were taken directly from, or are related to, recommendations in this series of reports. This series has also provided much of the information that the Department of Fish and Game and other agencies have used to justify acquisition of wetlands.

We believe that gaining control of wetlands is the best means of preserving and enhancing these areas, and providing for their public use. Control has been obtained by purchasing, leasing, or effecting a change in jurisdiction more favorable to natural resource maintenance.

In 1974 the U.S. Fish and Wildlife Service and the Department of Fish and Game issued a joint report entitled Acquisition Priorities for California's Coastal Wetlands. With that report we attempted to direct available funds toward acquisition of those wetlands we believed to be important and most in need of acquisition at that time. The priority setting criteria included the overall habitat value to fish and wildlife, the occurrence of endangered species, and the potential threats from development.

A number of agencies including the Department of Parks and Recreation, U. S. Fish and Wildlife Service, the Coast Commission, and of course the Department of Fish and Game, have used the priority list. In effect we have cut up the pie, with the above-mentioned agencies assuming acquisition reponsibilities for different areas. As a result, of the top 25 areas identified in the report, actions have already been, or will soon be, taken to acquire 15 of them. Since our initial acquisition at Buena Vista Lagoon we have purchased or otherwise gained control of 11 areas. We have spent nearly $6 million acquiring about 2200 acres of wetlands which comes to $2700/acre.

Of course, we were quite fortunate that shortly after we published the "Acquisition Priority" report several sources of funds became available to us and to other agencies. The largest source of funds to us and to the Department of Parks and Recreation was the 1974 Park Bond Act and the more recent 1976 Park Bond Act. The Wildlife Conservation Board, the acquisition arm of the Department of Fish and Game, received $10 million in 1974 and $15 million in 1976 from the Bond Acts. Most of the monies of the 1974 Bond Act and at least $10 million of the 1976 Bond Act are earmarked for coastal acquisition projects. In addition, we obtained a $3.4 million special appropriation from the legislature to acquire Upper Newport Bay. This was part of the 4.5 million-dollar settlement the state received from the Santa Barbara oil spill. The remaining $1.1 million will be used for habitat improvement and development of public use facilities at Newport Bay. While the state appears to be quite well off now, having a fairly large amount of money for acquiring coastal wetlands, the U. S. Fish and Wildlife Service has not fared as well. While they have approval to acquire lands within the boundaries of several established refuges, the monies to acquire lands have been slow in coming.

To summarize the money situation—it is good as far as the state is concerned. And, in my opinion, with the combined efforts of the several state departments and local agencies who have received monies from the 1974 and 1976 Bond acts, most of the more important coastal wetlands will be placed in public ownership.

Most of the coastal wetland areas over which the Department of Fish and Game has gained control, either by purchase or through action of the State Lands Division and Commission, have been classified as ecological reserves. This means that the primary purposes of areas so classified are to preserve the habitat along with the fish and wildlife there for public observation and scientific study.

Operational plans for maintenance and use of the coastal wetland areas acquired during the last 8 years have been developed. However, few such plans have been implemented, because most available funds continue to be directed toward acquisition. Our management of those areas has been limited to posting and to requesting regulations for the Fish and Game Commission to control public use. Most of our wetland areas do not require an intensive program of maintenance or restoration. We are, however, proceeding with plans to reestablish about 150 acres of marsh at Bolsa Chica and to improve tidal flooding in Upper Newport Bay. Additionally, since both of these areas are within a few minutes of downtown Los Angeles we are also planning to provide facilities for public use. At Upper Newport Bay we are proposing to build an interpretive center which we estimate will be visited by about ½ million people annually. The habitat improvements and public use facilities will cost us over $1 million at Newport. Our marsh recreation project at Bolsa Chica will cost us about $750,000, including moderate public use facilities.

In summary, the efforts of public agencies and an interested and concerned citizenry during the last decade have accomplished much toward preservation and maintenance of the state's coastal wetlands resource. The Department of Fish and Game has taken a lead role in this effort through its informational program, primarily directed at decision makers in all levels of government. With the passage of the 1974 and 1976 Park Bond acts, the Departments of Fish and Game and Parks and Recreation have received $25 millions for wetlands acquisition and have proceeded to acquire a substantial portion of wetlands remaining in private ownership. With the presently planned acquisitions by state, federal, and local agencies, most of the State's coastal wetlands resources will receive protection. The next step in the process of coastal wetlands protection, which has been somewhat neglected to date, is to devote more effort to improve these areas for wildlife as well as to provide public use and enjoyment.

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SHOREBIRD CENSUS STUDIES IN BRITAIN

A. J. PRATER[1]

ABSTRACT.—Studies on shorebirds in Britain and Europe involve the combination of extensive census and intensive banding data. Although such studies are still in an early stage of development, they do provide information needed for effective conservation planning. This paper outlines the techniques used and provides examples of the results which can be obtained on distribution, migration, population fluctuations, and detailed characteristics of each species.

Counts of wildfowl have been made for many years and much information is now available on distribution, migration, and aspects of population dynamics. There is therefore a considerable fund of knowledge on which conservation assessments can be based. On the other hand, shorebirds form a significant proportion of the total avifauna on estuaries and other coastal areas and, in winter, many species utilize only these habitats. Yet, until recently there were no extensive data on the numbers and distribution of passage and wintering shorebirds.

During the last ten years several large development schemes have been proposed for some of the major estuaries in Britain and elsewhere in Europe. These areas were considered to support large numbers of shorebirds but neither the precise number involved nor the relative national or international importance was known. The evaluation of these aspects was considered to be important in efforts to obtain a balanced conservation program. The counts also provided data on fluctuations in numbers of birds between successive years.

The three principal voluntary ornithological bodies in Britain, the British Trust for Ornithology, the Royal Society for the Protection of Birds, and the Wildfowl Trust, joined together to provide the manpower and expertise to carry out the 'Birds of Estuaries Enquiry.' The project was financed by the Nature Conservancy, now the Nature Conservancy Council and the Institute of Terrestrial Ecology. Comparative international data were made available from the Irish Wildbird Conservancy's 'Wetlands Enquiry' and the counts elsewhere in Europe and Africa were obtained by the International Waterfowl Research Bureau's (I.W.R.B.) Wader Research Group.

METHODS

COUNTS IN BRITAIN

Counts were made on almost every estuary within Britain between August 1970 and May 1975; additional data were obtained during a pilot survey between August 1969 and April 1970. All larger estuaries in Britain were counted regularly and additional information was gathered on most small estuaries, larger coastal bays, and sections of rocky coastline. Data were obtained on about 180 areas within Britain.

The counts were made once a month, although for some areas additional data were obtained, and were synchronized with a weekend spring tide. The counts on all larger areas were made during the period two hours either side of high water, when the shorebirds were moving to, on, or dispersing from their high tide roosts. It was possible to count small, narrow areas during low water when the shorebirds were dispersed on their feeding grounds. The counts were obtained mainly by experienced amateur birdwatchers but some data were provided by professional ornithologists. To obtain fully coordinated counts a series of regional organizers were appointed, and for each complex there was a local count organizer who dealt directly with the individual observers, up to 30 of whom were involved

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in counting a major estuary. In this way it was possible to ensure as complete coverage as possible in every month.

The accuracy of the estimates made by all counters, almost 1000 of whom have participated, could not be measured. Checks have been made in two of the important areas: Morecambe Bay (Wilson 1971) and the Ribble (Hale 1974). They measured both the accuracy and consistency of the counts by comparing aerial and ground photographs with numbers observed at the same time. Counters have a tendency to consistently underestimate shorebird flocks. For the larger species and flocks of less than 1000 of the smaller species the estimate was low by 5–10%. Large flocks of smaller species, mainly *Calidris* sp., may be underestimated by up to 25%; however, because the period of observation averaged 2–3 hours, the observer was able to either count small flocks joining or leaving a roost and was rarely confronted with very large flocks. The other potential source of error was the failure to locate all birds within the area. On a few occasions this clearly formed a major source of error, but once the observer has covered the counting area for a season (10–12 counts) all roost sites will have been located.

Now that data for six years have been obtained, a detailed assessment of each site is being made and the number of counts reduced to three each winter (December, January, and February) to monitor annual changes in the numbers and distribution of shorebirds.

INTERNATIONAL COUNTS

Since 1966 the I.W.R.B. counts of shorebirds have been organized in a way similar to the counts of the 'Birds of Estuaries Enquiry.' Each country in northwestern Europe has a national organizer and regional teams of observers. The counts made in Ireland by the Irish Wildbird Conservancy closely followed the British program but the international counts elsewhere were carried out only in January, although partial data were also obtained during August/September and April/May. In January expeditions visited other countries in southern Europe, Africa and Asia where there were no counting organizations. The aims of the international counts were twofold: firstly, they provided an estimate of the total population and distribution of each species of shorebird, from which could be obtained an objective assessment of the importance of each area. Secondly, the regular midwinter counts provided a method of monitoring the fluctuations of each species. The international counts are continuing both with regular European counts and expeditions visiting further unworked regions.

BANDING DATA

Census information can be greatly enhanced in value by combining it with banding data. This is clearly true in migration studies: Results from banding activities provide data on the breeding populations involved, on the use made of each area by different components of each population, and on the mobility characteristics of each species. These are all aspects which provide a more accurate conservation assessment at both site and species levels.

Since 1967 banding data (age, molt, measurements, weights, recoveries, and retraps) have been obtained from a large number of shorebirds. Up to the end of 1975 almost 500,000 shorebirds have been banded in Britain and Ireland and currently between 30,000 and 40,000 are banded annually. Over 10,000 individuals of seven species of shore waders (Dunlin *Calidris alpina*, Oystercatcher *Haematopus ostralegus*, Knot *C. canutus*, Redshank *Tringa totanus*, Ringed Plover *Charadrius hiaticula*, Curlew *Numenius arquata* and Sanderling *C. alba*) have been banded. In the rest of Europe large numbers have also been banded. In 1970 the British Trust for Ornithology set up the Wader Study Group to help liason between banders in Britain and elsewhere and to encourage further studies. By helping cooperative effort and by aiding special expeditions to catch shorebirds in other countries, from Greenland and Norway south to Mauritania, it has been possible to interpret data gathered in northwest Europe.

RESULTS

The six years of counts have provided much information. It is not intended in this review paper to describe them all in detail but to illustrate some of the results arising from extensive and intensive counts. The principal examples will be drawn from the counts of the Knot, the European wintering population of which breeds in northern Greenland and northeast Canada.

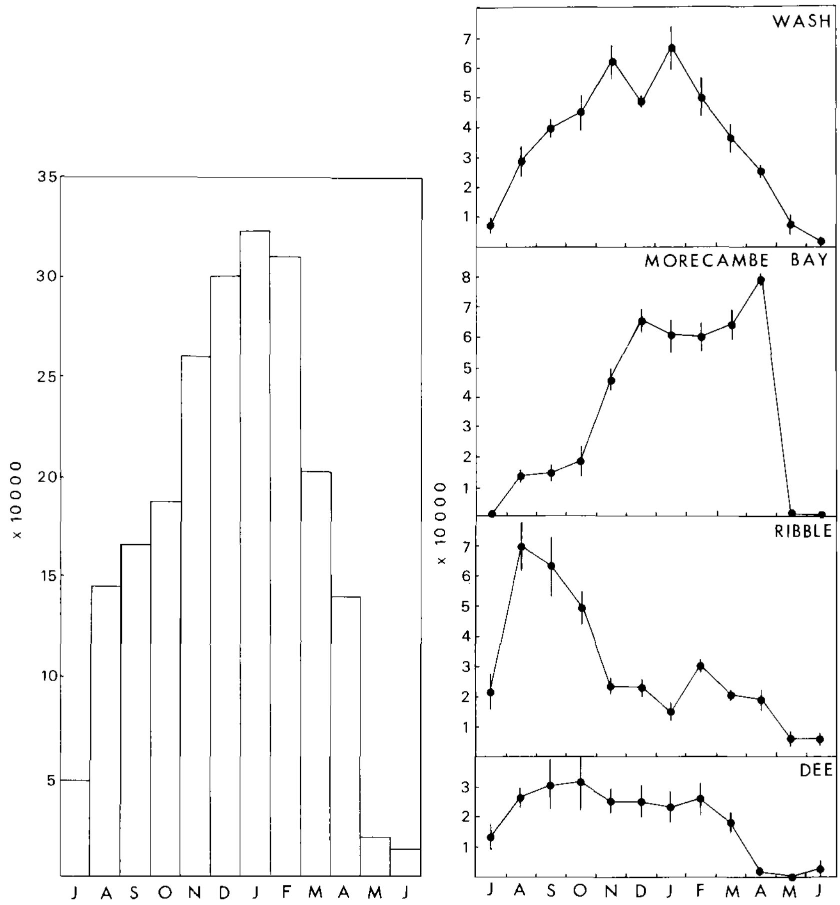

FIGURE 1. Left: Average number of Knot in each month in Britain and Ireland. Based on summation of average monthly counts in each estuary 1969–75. Right: Number of Knot in each month on the principal British estuaries. Filled circles, mean numbers; vertical bars, standard errors; based on 3–6 counts.

Number on Each Estuary

There are always small variations in the extent of coverage between years due to adverse weather conditions or illness or changes in the circumstances of observers; this precluded, in this study, a simple averaging of the annual monthly counts to provide a national picture. Instead the occurrence of the Knot on a national level (Fig. 1) has been obtained from the summation of the average monthly counts for each wetland.

The average counts of Knot from the four most important estuaries are also presented in Figure 1. Although the standard error is usually 10–20% of the mean, this might be expected in high arctic species which have considerable annual fluctuations in numbers. For example, in winter, at the time of maximum counts, the total numbers of Knot counted varied between 423,000 in 1971–72 to 237,000 in 1974–75.

Of particular note is that, even on major areas for a species, the pattern of

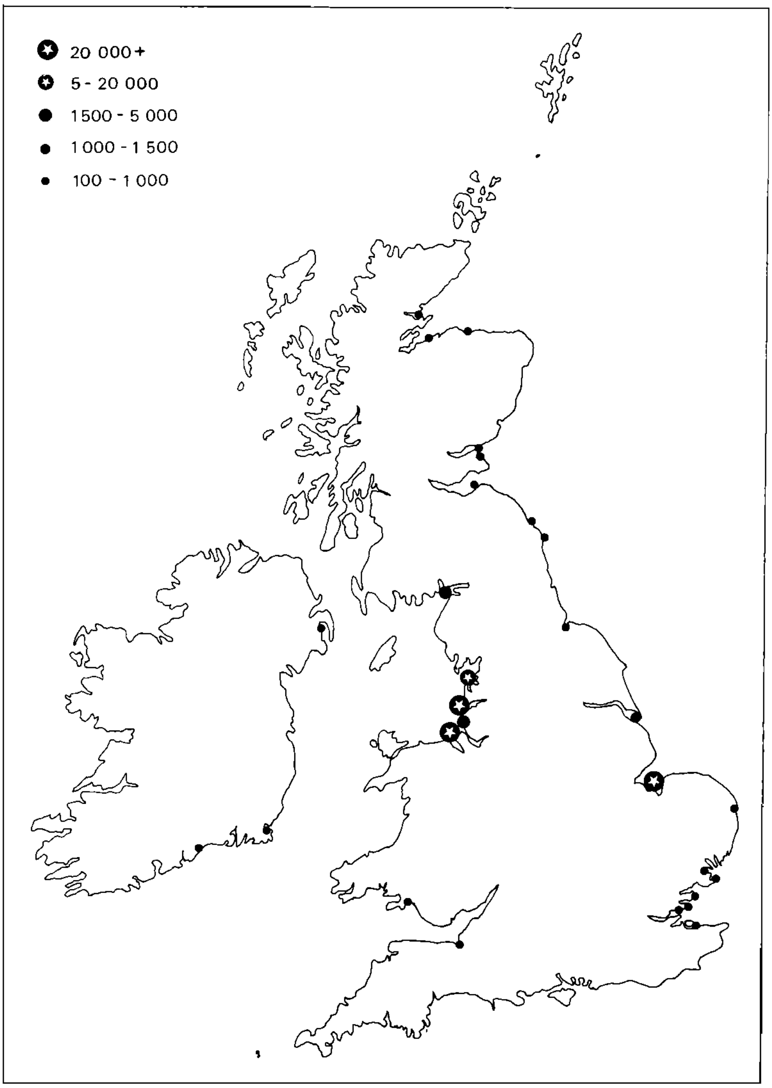

FIGURE 2. Distribution of Knot in Britain and Ireland in autumn. Based on average numbers present in August/September. Circles with stars are estuaries of international importance, larger filled circles are national importance (during autumn), smaller filled circles are of regional or local importance.

occurrence may neither follow a similar form nor correspond to the national picture. In a study in Essex, significant correlations have been found between numbers counted and biomass of preferred foods in each estuary (Goss-Custard et al., 1977). These highlight the value of and the need for the extensive collection of data.

The numbers counted in each month on each estuary or in the whole country provide, when compared with similar data for other regions, a picture of the migration pattern of the species. In Britain there is a rapid build-up of Knot in autumn, then the adult birds molt and numbers are relatively stable until this

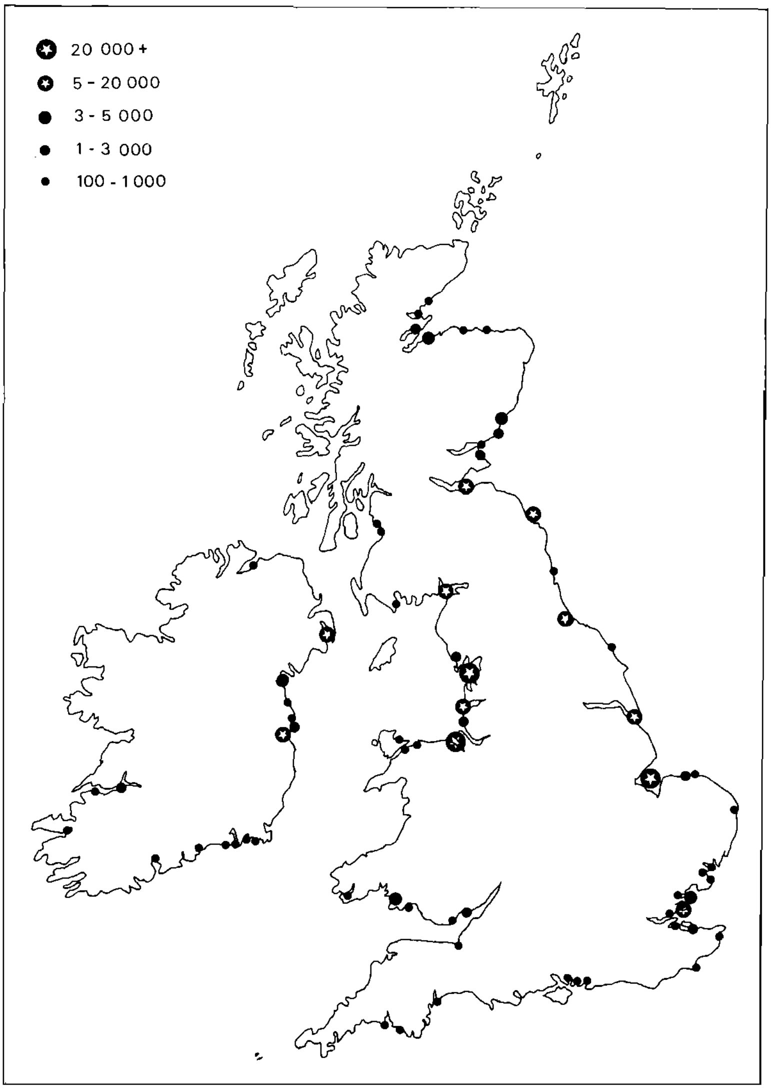

FIGURE 3. Distribution of Knot in Britain and Ireland in winter. Based on average numbers present in January. Symbols as Figure 3 but note level of national importance differs as more birds are present.

has been completed by mid-October; after that numbers rise quickly to a mid-winter peak. The peak in Britain and Ireland corresponds to a trough in numbers in the Waddensea (Denmark, Federal Republic of Germany, Netherlands) (Prater 1974).

NATIONAL DISTRIBUTION

The national distribution of each species can be illustrated in several ways, but perhaps a simple map is the clearest method of presenting the information, especially if it is aimed at environmental planning authorities. If monthly counts

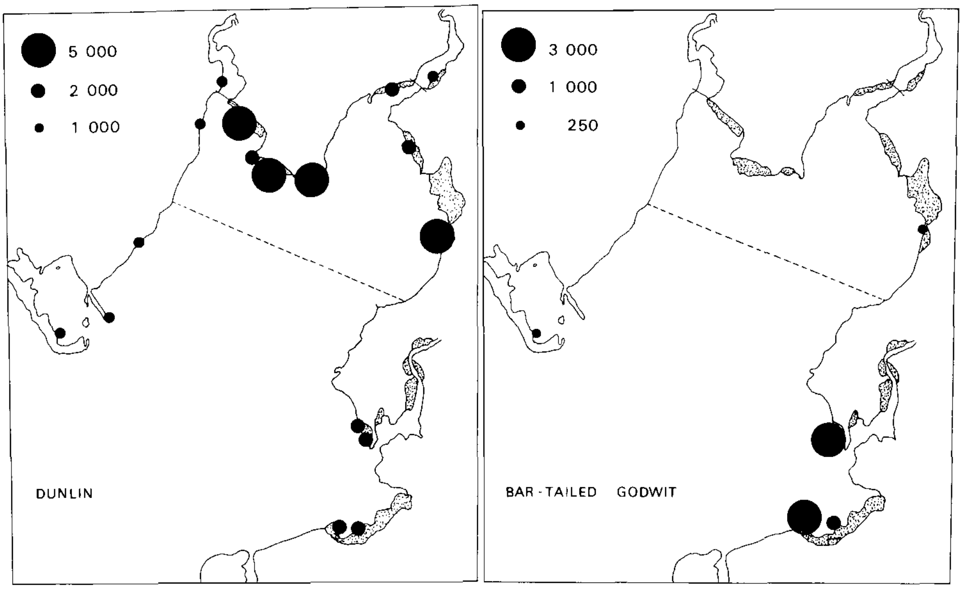

FIGURE 4. Distribution of Dunlin and Bar-tailed Godwit in Morecambe Bay in relation to a proposed barrage (dotted line). Salt marshes are stippled.

have been made the changes in distribution with season can be demonstrated. Figures 2 and 3 present the distribution of Knot in autumn and winter in Britain and Ireland. In September, when adults are molting, the species is found in only a few major estuaries but with the influx in winter there is a rapid increase in numbers in other estuaries.

DISTRIBUTION WITHIN EACH ESTUARY

The distribution of shorebirds within each estuary was also mapped. Where possible, feeding grounds were noted by the observers. The roost sites changed with the tidal cycle. On neap tides shorebirds formed roosts near to their feeding grounds; these were also usually used as subroosts during the spring tides. The numbers of each species of shorebird were obtained separately for each roost. Thus it was possible to map the distribution of each species in detail. This information was essential for the detailed assessment of the possible impact of estuarine developments. Figure 4 shows the distribution of Dunlin and Bar-tailed Godwit *Limosa lapponica* in Morecambe Bay (from Wilson 1971) and the position of a proposed barrage [dam] across the estuary. The latter species would be little affected but the feeding grounds of 31,000 out of 42,000 Dunlin would be lost. On the Wash, Goss-Custard (1977) has used count data with detailed observations to assess the relative impact of different sites for a proposed reservoir.

CHANGES IN NUMBERS

Shorebird numbers are not static. They change annually due to factors which appear to be linked to climatic variations. In Britain severe winters have caused high mortality (Dobinson and Richards 1964) but no prolonged cold weather has occurred since 1969 when shorebird counts started. Raptor predation appears to

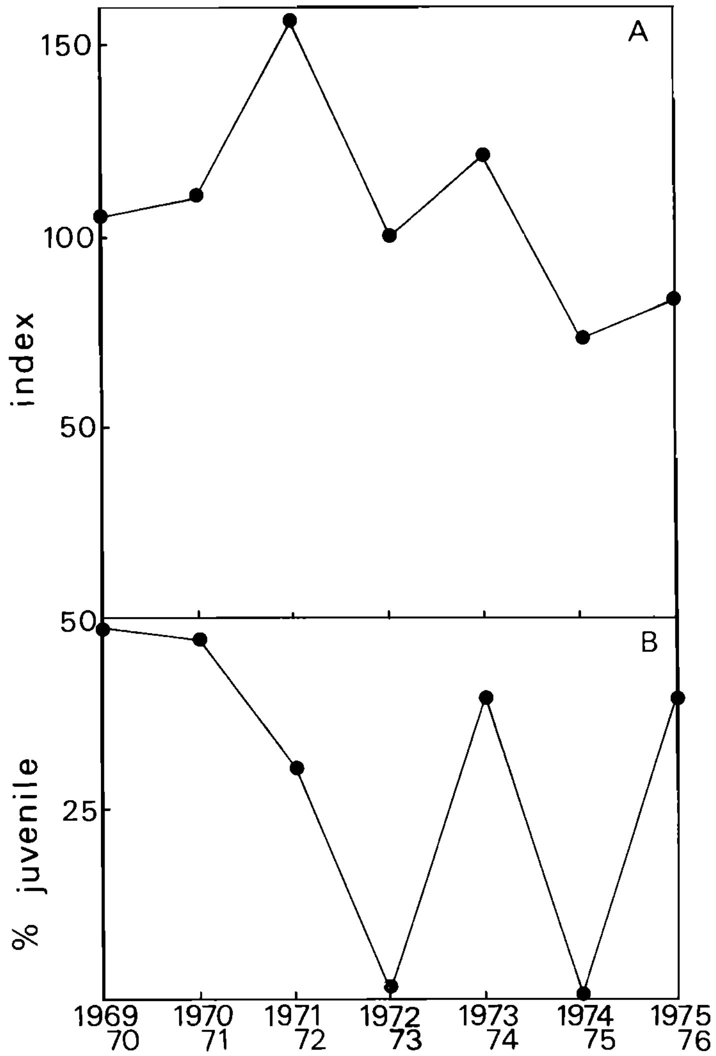

FIGURE 5. Relative changes in the number of Knot wintering in Britain and Ireland and percentage of juvenile Pale-bellied Brent Geese wintering in Ireland.

be unimportant in Britain, unlike the situation in California (Page and Whitacre 1975), and most shorebirds have been fully protected from hunting since 1954. The changes in numbers of Knot are presented in Figure 5. The index was calculated using paired samples and relating them to a standard year; 1972–73 was chosen as it was the second winter with full coverage. A considerable variation is shown from 155 in 1971–72 to 74 in 1974–75. The index is compared in Figure 5 with the breeding success of the Light-bellied Brent Goose *Branta bernicla hrota* as observed by winter age ratios in Ireland (data from the annual goose reports in 'Wildfowl'). This species breeds in a similar zone to the Knot. Barry (1962) has described the effect of late spring/summer weather conditions on this species. In some years breeding may not take place. It is assumed that broadly

TABLE 1
PERCENTAGE OF FIRST WINTER KNOT IN THE TWO REGIONS OF MORECAMBE BAY

Winter (Nov–March)	Walney/Keer/Lune			Kent/Leven		
	Adult	IW[a]	%IW	Adult	IW	%IW
1968–69	3495	175	4.8	47	23	32.9
1969–70	1894	132	6.5	156	334	68.2
1970–71	432	22	4.8	294	50	17.0
1971–72	126	3	2.3		ND[b]	
1972–73	354	20	5.3	1031	168	14.0
1973–74	90	2	2.2		ND	
TOTAL	6391	354	5.2	1528	575	27.3

[a] IW, first winter.
[b] ND, no data.

similar conditions will affect the Knot, although the precise effect will be slightly different. There is a close agreement between breeding success of Brent and the trends in the winter numbers of Knot with sharp decreases occurring in the two winters (1972–73 and 1974–75) which were preceded by very poor Brent breeding seasons. During this period the number of Knot wintering in France has also decreased from an estimated 100,000 to 10,000 and in the Waddensea from 70,000 to 40,000.

Unfortunately no long-term shorebird census data are available, so the changes observed recently can not be placed fully in context. In Britain there are many local societies which have published detailed bird records since the 1930's. The Black-tailed Godwit *Limosa limosa* (the subspecies occurring in Britain is *L. l. islandica*) was rare in winter in the early years and a fairly complete record exists of its changes in numbers. Prater (1975) showed that there was a slow increase in numbers; there were less than 20 in 1931–35, 310 in 1941–45, 1440 in 1951–55, 3200 in 1961–65 and 3730 in 1971–75. There were some indications that a peak occurred about 1970 and numbers may now be declining slightly. This increase corresponded to the climatic amelioration and spread to new breeding areas in Iceland (Gudmundsson 1951). Both long- and short-term trends in numbers are no doubt continuing and this means that population estimates and hence criteria of international and national importance have to be revised periodically (see Discussion).

INTERPRETIVE STUDIES

The inclusion of banding with census data provides a much more precise understanding of the role that each wetland plays in the life cycle of the species. In particular it provides the age, sex, race, and molt status of the species. The weight changes may indicate when an increased food demand occurs, and the pattern of retraps (birds found on the same estuary) and recoveries (birds found elsewhere) may give a measure of the mobility of the species.

There is little information on the distribution of sexes of shorebirds in Britain. However, virtually all of the Ruff *Philomachus pugnax* wintering in Britain are males, whereas in South Africa about 90% are females (Schmitt and Whitehouse, 1976). Further examples may be found in future studies.

The difference in timing of adult and juvenile migration periods is well known but there are many other examples of age segregation in shorebirds. Table 1 presents the winter data for Knot in Morecambe Bay. This period was chosen to eliminate biases arising from the trapping of flocks of juveniles during the autumn migration. Observations of movements enabled five subdivisions of the area to be made. Three of these have a very low percentage of first winter birds (Walney 4.7%, Keer 5.4%, Lune 4.0%) whereas the two areas in the north of Morecambe Bay had much higher percentages (Leven 27.1%, Kent 32.9%). These differences were consistent in successive years.

Racial or population discrimination is also an important aspect of shorebird studies. Much work is in progress at present on geographical variation, using both biometrics and plumage characters. Once the passage and wintering areas of each population are known, or the percentage contribution of each where overlap occurs, the counts provide an estimate of that population. Dick et al. (1976), using bill measurements, showed that the African wintering Knot breed in the USSR while the west European birds breed in Greenland and Canada. The effect of development schemes would be felt to different degrees by different populations.

Other studies are being made on the mobility characteristics of each species of shorebird. All species studied show a high specificity to estuary in successive years and also to site within each estuary within a single winter. There are, however, differences between species. The same winter movements of two species have been studied in Morecambe Bay. Preliminary studies, based on the proportion of available birds retrapped from a series of large catches all around the estuary, indicate that although the Knot is more likely to remain in a single area throughout the winter, up to 20–40% may move away. Dunlin is much more site specific and only a single bird was retrapped away from the ringing site. A similar pattern appears to be shown for successive years. On the Wash the Knot and Oystercatcher are the species which are least site specific and it is possible that this behavior has been evolved to exploit the relatively variable food source of bivalve molluscs which do not have a constant settlement pattern.

DISCUSSION

The main aim of the 'Birds of Estuaries Enquiry' was to provide a conservation assessment of all estuaries. I.W.R.B. counts provided an estimate of the total population of each species found in Europe and North Africa (Prater 1977). At the 5th International Conference on the Conservation of Wetlands and Waterfowl, Heiligenhafen 1974, the governmental delegates agreed that a site was of international importance if it supported 1% or more of the total flyway population (here it refers to the Atlantic coast of Europe and northwest Africa) of any species of shorebird. This should only be used if the numbers exceed 10,000, so that 1% is 100 or more. The total number of Knot of this flyway is about 600,000 and using the 1% criterion for this species, the Wash and Ribble estuaries are of importance from July to May, the Dee from July to March and Morecambe Bay from August to April. These four estuaries supported between 21.2% and 28.2% of the flyway population of Knot between August and April. Similar calculations can be made for other species which occur.

The 1% criterion can be used throughout the year if the species winters almost completely within the area covered by the January counts. Counts made during spring or autumn migration can, if carefully designed, also provide total population estimates for species wintering wholly or partly outside the winter census area.

There are several other criteria of international importance which apply to waterbird populations. Total shorebird numbers of 20,000 or more at one site is also considered to represent a figure of international importance. Special rarity criteria should be used if the flyway numbers are less than 10,000. Most other criteria relate to the wetland, whether it is unique, representative, or an important research area.

The numerical criteria do not necessarily relate to the survival of the species, as many other factors interact to affect this, but they do highlight the sites where significant numbers of birds occur and where loss of habitat would have a noticeable effect. All numerical criteria need to be constantly revised as there are changes in the overall population numbers.

It is possible and probably desirable to use similar criteria on a national scale to show which estuaries are of the next level of importance. In Britain 1% and 10,000 are those accepted; the 10,000 is, like the 20,000 international, probably the less useful criterion as it does not take into account the species involved. Because monthly estimates have been made in Britain it is feasible to assess the importance of each site on a national basis throughout the year.

ACKNOWLEDGMENTS

The information presented in this paper was obtained by the efforts of about 2000 observers and banders throughout Europe; it is to them that the greatest thanks must go. I would also like to thank my colleagues, in particular Dr. L. A. Batten, Dr. J. D. Goss-Custard, and J. Parslow for their continuing help and advice. The survey was financed by a grant from the Nature Conservancy Council.

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EFFECT OF HABITAT LOSS ON THE NUMBERS OF OVERWINTERING SHOREBIRDS

J. D. Goss-Custard[1]

Abstract.—This paper discusses issues raised by attempts to predict whether the numbers of shorebirds using an estuary will decrease following industrial, agricultural, or recreational development of some of their feeding grounds. Within an estuary, most feeding is usually done in limited parts of the shore where the prey are most abundant. Hence, the siting as well as the size of a development scheme is important in evaluating its effects on particular shorebird species. Bird densities may be highest in those estuaries where prey densities are highest but it is not clear if this reflects a simple behavioral preference of individuals for the best feeding areas or results from disproportionately high mortality rates, or subsequently low reproductive output, in estuaries where food is scarcest, or is due to a mixture of both. Hence studies need to be designed to see if a loss of feeding grounds will lead simply to a redistribution of birds over the feeding grounds or to a reduction in overall numbers. Observations suggest that bird density may reach a ceiling level in preferred areas so that a loss of habitat would cause more birds to feed in the less favored areas or even to leave the estuary altogether. However, some increase in numbers in the preferred areas that remain may nonetheless take place. Several indirect lines of evidence suggest that food shortage may be a contributory factor to winter mortality, especially during very cold weather. Field studies indicate that all the ways in which birds might respond to a loss of feeding grounds within an estuary would reduce the rate at which they can feed and so exacerbate any food shortage. Some of the difficulties in predicting the effect of a loss of feeding areas on shorebird numbers are discussed.

This paper discusses some issues raised by attempts to predict whether the numbers of shorebirds using an estuary will decrease following a reduction in their feeding grounds when parts of the shore are developed for industrial, agricultural, or recreational purposes. It refers mainly to studies carried out in Britain where shorebirds occur in their greatest numbers outside the breeding season (August to May) and many of the estuaries are of international significance for migrating and overwintering birds (Prater 1975). The work was done on several estuaries along the east coast, but the paper focusses particularly on the Wash where a proposal has been made to build an impoundment on the shore for storing fresh water (CWPU 1976).

IMPORTANCE OF THE FEEDING AREAS

Shorebirds are not normally spread evenly over the intertidal flats of an estuary. Rather, some areas are used more than others. The most preferred feeding grounds may be the ones where the birds can feed at the fastest rate (Goss-Custard 1970a, 1977a, b), provided that they are not so far from the roosts occupied at high water that the amount of energy expended in reaching them renders less rich areas nearer to the roost more profitable to exploit (Zwarts 1974). On the Wash, for example, most species fed in only a small part of the intertidal flats and the areas used varied between species, largely according to the distribution of prey organisms. Consequently, a limited development on the shore would affect species to different extents. Figure 1 shows how one of the proposed reservoir schemes would remove a large part of the feeding grounds of the Knot, *Calidris canutus* (L.), but would leave the areas used by the Bar-tailed Godwit, *Limosa lapponica* (L.), virtually untouched (Goss-Custard et al. 1977a).

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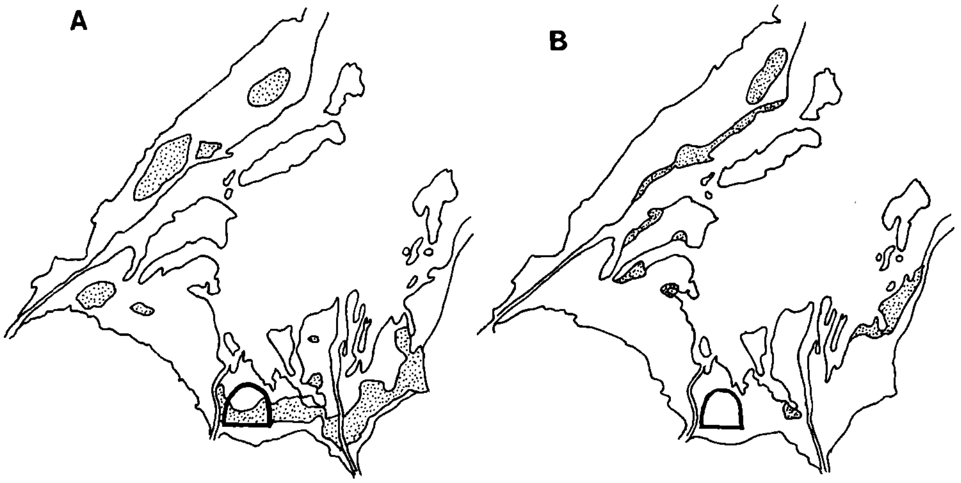

FIGURE 1. The feeding areas of Knots (A) and Bar-tailed Godwits (B) on the Wash, east England. Shaded areas show the feeding grounds mainly used once the receding tide had exposed them. Thick black line shows the limits of one of the proposed reservoir schemes (Wingland).

Predictions on the effect of a loss of feeding area are required, of course, for those cases where large parts of the existing feeding areas would be lost and it is unlikely that new feeding grounds would accrete elsewhere to replace them. The problem, however, is that the role which these feeding grounds play in the population dynamics of shorebirds is not known, although there is some evidence to suggest that food abundance may be important in determining the numbers occurring in an estuary. The densities of Redshank, *Tringa totanus* (L.), and Curlew, *Numenius arquata* (L.), were correlated with the densities of their main prey species when nine estuaries and coastal flats in southeast England were compared (Goss-Custard et al. 1977b). Figure 2, for example, shows the relationship between (i) the mean winter density of Curlew based on monthly counts of each estuary from November to March, and (ii) the combined numerical densities of the two principal prey species, the polychaete worm *Nereis diversicolor* O. F. Müller and the bivalve mollusc *Scrobicularia plana* (da Costa).

Such a correlation may reflect a close adjustment of bird numbers to food abundance arising through disproportionately high rates of mortality, or subsequently low breeding output, amongst birds wintering where food is scarcest. In this case, a reduction in food abundance following a loss of habitat would probably lead to a further decrease in bird numbers. Alternatively, the correlations may simply reflect a preference by individual birds for the best feeding areas, as seems to occur within a single estuary (Goss-Custard 1970a, 1977a, b), so that the birds merely respond behaviorally to the different levels of food in the various estuaries. In fact, the association between bird and prey densities occurred in autumn as the birds returned from the breeding grounds at a time of year when British shorebirds seem to experience little difficulty in obtaining their food (Goss-Custard 1969, Heppleston 1971, Goss-Custard et al. 1977c). If this is the case, a loss of feeding grounds in one estuary may simply lead to a redistri-

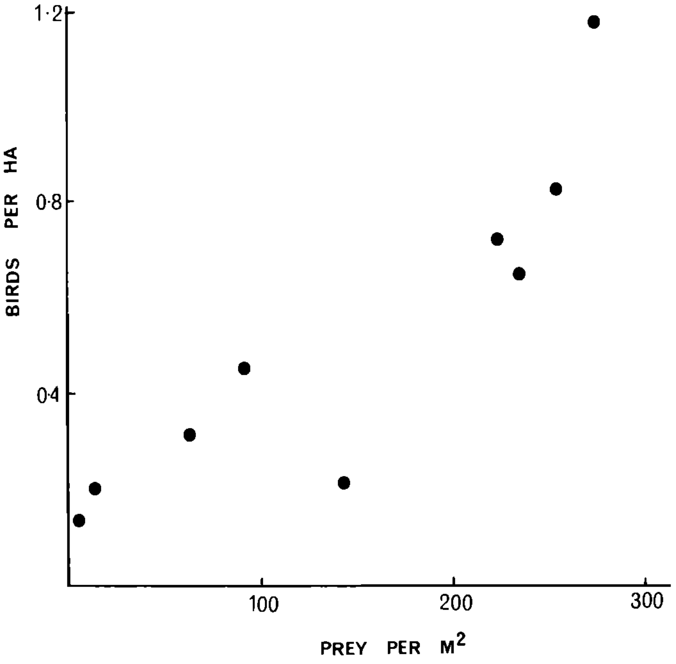

FIGURE 2. The mean winter density of Curlew on each of nine estuaries in relation to the combined densities of their main prey, *Nereis diversicolor* and *Scrobicularia plana*.

bution of birds between estuaries rather than to a reduction in overall numbers. However, it is possible that the correlations reflect both behavioural responses of individuals to spatial variations in prey density and area differences in survival related to food abundance, especially if different sections of the population behave in different ways. Thus, young birds wintering in a region for the first time may move between estuaries to find areas where the chances of survival are greatest: in fact, some movement of birds between estuaries in southeast England has been recorded (Prater 1971, Goss-Custard et al. 1977b). In contrast, older birds may return to the area where they successfully survived the previous winter, and survival may be higher in those estuaries where food is most abundant each year: this would account for individuals being recorded in the same estuary in different winters, both in southeast England (Goss-Custard et al. 1977b) and elsewhere (Ogilvie 1963, Dare 1970, Kelly and Cogswell this volume).

Although usually hindered by being of limited duration and restricted only to the estuary in question, much of the research in environmental impact studies is designed to distinguish between these possibilities. But at the present state of knowledge, predictions on the effects of a loss of habitat are necessarily made without a full understanding of the population biology of the species concerned and, in particular, of the role played by the food supplies outside the breeding season. Nonetheless, studies of (i) the behavioral responses of the birds to their own density and to that of their prey, and (ii) the possibility that some birds already have difficulty in obtaining their food requirements, may provide a basis for prediction.

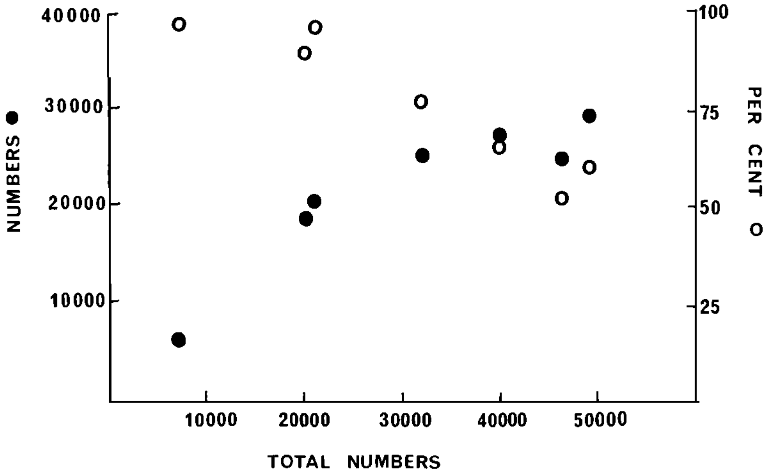

FIGURE 3. The numbers (●) and proportion (O) of Knots on the preferred feeding grounds in relation to the total numbers of birds present.

DENSITY-RELATED BEHAVIOR

Studies in Holland (Zwarts 1974) and in Britain (Goss-Custard 1977a, b) on the sequence in which shorebirds occupy their feeding grounds as their numbers increase suggest that the densities of several species may reach a maximum or ceiling level in the preferred parts of the habitat. For example, on the eastern half of the Wash, most of the small number of Knots present in late summer occurred in one place (Fig. 3). An increasing proportion fed in the less favored areas as the total numbers rose in the autumn, suggesting that there was a resistance to a further rise in density in the preferred areas. A linear increase in the proportion of birds feeding in the poorer areas means that the numbers in the preferred areas will eventually reach a ceiling level and, in fact, the numbers there did rise at a decelerating rate until substantial increases in overall numbers produced only a small rise in density.

The mechanism underlying this apparent density limitation has not been investigated. However, it seems that the spreading out need not necessarily involve overt aggression between birds even though Knots did fight over food items and feeding sites at an increasing rate as their density increased (Goss-Custard et al. 1977c). On the Ythan estuary, for example, Redshank spread out from the most profitably exploited parts of the shore when large numbers of birds were present even though aggressive interactions were not seen (Goss-Custard 1977b). Apparently, birds simply avoided areas of high bird density, perhaps to reduce the various forms of interference which may occur when birds forage at high densities (Goss-Custard 1970b, 1976).

These observations imply that there would be a limit to the numbers of birds that could exploit any preferred feeding areas that remain after a development has taken place and indicate that more feeding would be done, presumably by subdominant individuals, in the less suitable areas. Indeed, a reduction in feeding area might result in birds leaving the estuary altogether. The extent to which birds do both these things would depend on how close densities already were to

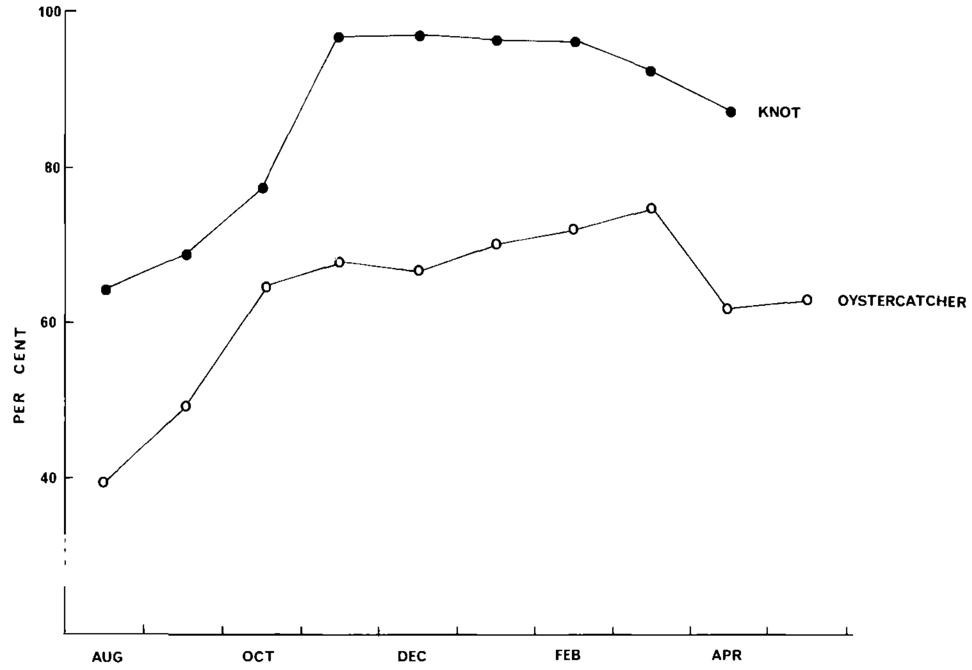

FIGURE 4. The proportion of the time during which feeding grounds were exposed in daylight that Oystercatchers and Knots spent feeding.

any ceiling levels that exist and this is likely to vary both between species and situations. Studies of Oystercatchers, *Haematopus ostralegus* L., and Knots on the Wash, for instance, showed that a decreasing proportion occurred in the preferred areas as overall numbers increased so that a reduction in habitat could lead to both a redistribution of birds within the Wash and to emigration from the area altogether. However, it is expected that some increase in density above present levels might also occur in the preferred areas because in neither species, but especially in Oystercatchers, was a clear ceiling density reached and, in any case, an increase in competition for space might force birds to tolerate higher densities. Consequently, some increase in densities would probably occur in all the remaining feeding areas.

OCCURRENCE OF FOOD SHORTAGE

An increase in bird density may not affect survival unless birds already have difficulty in obtaining their food requirements at some time between August and May. On the Wash, shorebirds were between 3 and 10 times more likely to be found dead in winter than in autumn and spring, as were Oystercatchers elsewhere (Heppleston 1971). In contrast to some North American estuaries (Page and Whitacre 1975), predation on shorebirds in Britain seems to be of minor significance so that food shortage may indeed be implicated in the winter peak of mortality either directly or by reducing resistance to disease. Strong evidence of this is difficult to obtain, but the following kinds of indirect evidence, mainly from the Wash (Goss-Custard et al. 1977c), are suggestive.

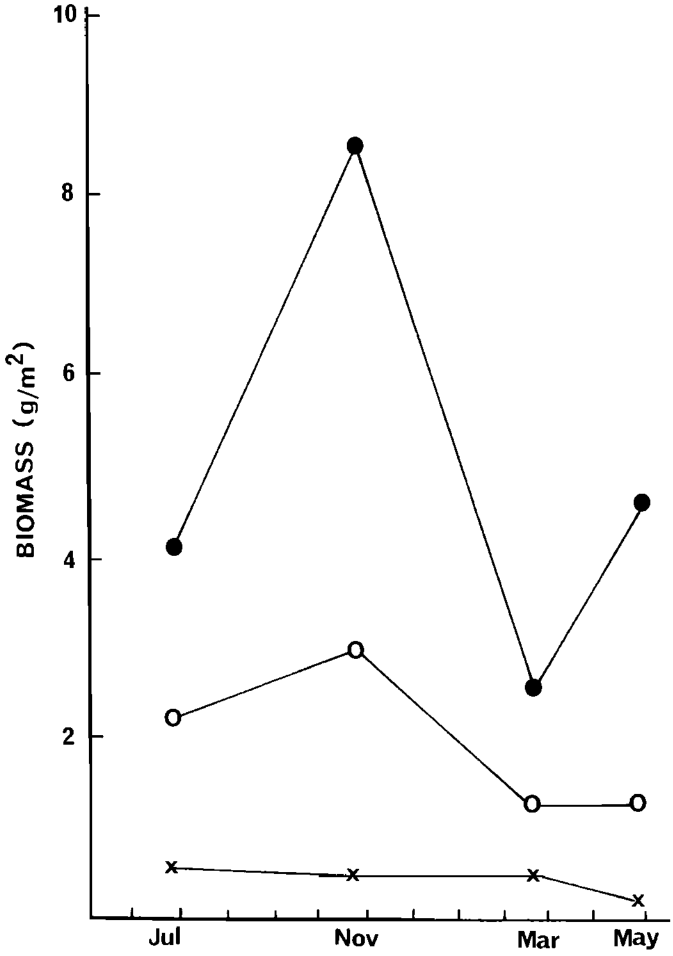

FIGURE 5. The biomass density of the size range of *Macoma balthica* taken by Knots on the Wash (6–15 mm) in three areas sampled in July (as the birds began to return from the breeding grounds), in November and March (at the start and end of the winter), and in May (when birds leave to breed).

(i) In daylight in winter, most species fed for a very high proportion of the time when the feeding grounds were exposed by the tide (Fig. 4). Indeed the small waders, such as Knots, Dunlins, *Calidris alpina* (L.), and Redshanks, fed all day on neap tides when some feeding areas were available throughout the tidal cycle, even at high water. In contrast, the birds spent a considerable time resting in spring and particularly in autumn. Shorebirds can feed at night but on the Wash we were unable to determine whether or not most did so. Consequently, feeding may have seemed more intense in winter simply because the birds preferred to feed in daylight and had to compensate for the reduced daylength. However, studies elsewhere along the east coast of Britain on Redshanks (Goss-Custard 1969), Oystercatchers (Heppleston 1971) and Bar-tailed Godwits (Smith 1975) suggest (a) that many waders may feed at night in winter because they fail to obtain

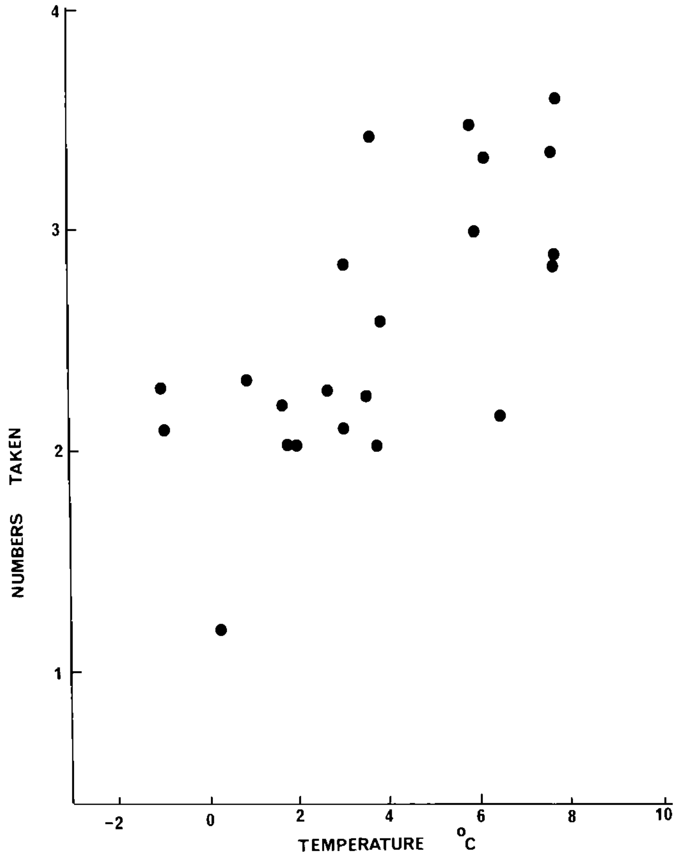

FIGURE 6. The numbers of bivalve molluscs taken per minute by Knots in relation to the temperature of the mud.

enough food during daylight and (b) that feeding at night occurs when the birds are also feeding intensively during the day.

(ii) The abundance of available food for several species declined during winter, suggesting that food may be relatively difficult to collect at that time of year. The decline was due to two factors. First, the actual biomass density of several important prey species decreased from a late summer or autumn peak to reach a low level by late winter or spring and the biomass of food consumed per unit time by waders depends in part on prey biomass (Goss-Custard 1970a, 1977a, b, Goss-Custard et al. 1977b). This winter decline was particularly marked in the preferred feeding areas where prey abundance was initially highest (Fig. 5). The decline can be attributed to (a) mortality (and perhaps emigration) of the restricted size range taken by shorebirds at a time when little replacement by growth from smaller size classes occurred, and (b) a decline in the biomass of individuals of a particular size: for example, some bivalves lost up to 40% of their weight during the winter. Second, the prey were least available or accessible to shorebirds in winter. The size classes of the bivalve mollusc, *Macoma balthica* L., taken by

Knots were buried much deeper in the mud in December than in autumn or spring and over 80% of the biomass present was below the depth at which the birds could reach it (Reading and McGrorty 1978). There were also more short-term variations in availability, superimposed on this long-term seasonal shift, which would make food more difficult to obtain in winter. The numbers of bivalves taken per minute by knots decreased sharply as mud temperature decreased (Fig. 6), presumably because the prey became less active and so more difficult to locate.

A decline in feeding rate at low mud temperatures has been observed in several other shorebirds (Goss-Custard 1969, Smith 1975). Along with the freezing over of large areas of mudflats, this tendency probably accounts for the large numbers of shorebirds found dead on many British estuaries during occasional prolonged periods of very cold weather (Dobinson and Richards 1964, Pilcher 1964, Pilcher, Beer, and Cook 1974, Goss-Custard et al. 1977c). While starvation is clearly implicated on these occasions, it is not yet apparent if such severe weather introduces acute difficulties which shorebirds do not normally experience or simply exacerbates a chronic condition of winter food shorage. Although requiring more research, the circumstantial evidence from the Wash and elsewhere indicates that at least a proportion of the birds of some species may have difficulty in obtaining food in winter, even in the absence of prolonged severe spells. By analogy with other groups of birds, it can be speculated that younger individuals, through being both inexperienced and subdominant to adults and so being harassed more and forced to feed in the less profitable areas, may be the ones most at risk.

EFFECTS OF INCREASED DENSITY ON SURVIVAL

The preceding two sections may be summarized as follows: (i) Following the loss of feeding areas in an estuary, some birds may move elsewhere but it is likely that bird density would nonetheless increase, especially in the less favored feeding areas. (ii) Shorebirds appear to have most difficulty in finding food in winter and food shortage may be at least a contributory factor to the winter peak of mortality, especially during very cold weather. This section discusses whether an increase in density on the feeding grounds would exacerbate the shortage of food and so increase mortality. In effect, this is really asking whether winter mortality is density-dependent, a possibility difficult to investigate directly because mortality is not easily measured. Consequently, studies are needed on the ways in which a rise in bird density could increase the birds' difficulties in finding enough food. Three possibilities can be identified.

(i) More feeding will probably be done in the less preferred parts of the shore where the rate of food intake may be relatively low. For example, on the Wash, most Oystercatchers fed where the biomass density of their main prey, the cockle, *Cerastoderma edule* L., was highest and the birds were able to obtain food at the fastest rate (Goss-Custard 1977a). Thus average feeding rate would decrease if birds fed more in the less favored parts of the shore.

(ii) A rise in bird density would be expected to increase the sometimes considerable impact which shorebirds (and other predators) may already have on their food supplies. On the Wash, shorebirds alone removed between 14 and 43% of the food supplies in the main feeding areas during the winter (Goss-Custard 1977a) and similar high rates have been recorded in other estuaries (Goss-Custard

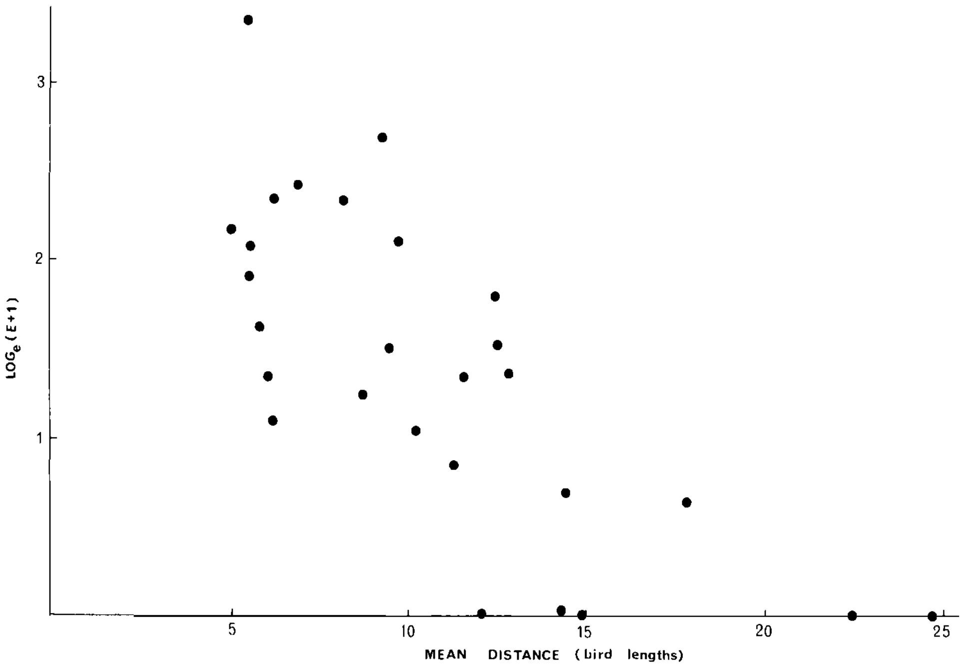

FIGURE 7. The numbers of encounters between Knots for food items on feeding sites in relation to their density. Encounter rate is expressed as number of encounters per 100 bird-minutes, and density as mean nearest neighbor distance.

1969, Smith 1975, Horwood and Goss-Custard 1977). Thus food abundance, and so the rate at which birds can feed, would probably decrease still further if an increase in bird density occurred. While the more rapid growth of individuals might enable the prey populations to some extent compensate for this added loss in autumn and spring, this is unlikely to occur in winter when growth usually ceases. The long-term effects of an increase in bird numbers are particularly difficult to evaluate, but studies in the Burry Inlet, South Wales, suggest that any sustained increase in predation by Oystercatchers would substantially decrease the abundance of cockles in the long term (Horwood and Goss-Custard 1977).

(iii) A rise in bird density would probably increase any interference that occurs between feeding birds. Interference may happen in two ways. First, birds may fight over food items or feeding sites. For example, on the Wash Knots contested bivalve molluscs, principally *Macoma*, at a rate which increased as their own density increased (Fig. 7). Although the evidence that such fighting significantly reduced average feeding rate is equivocal, the effects of an increase in fighting may fall disproportionately on subdominant individuals so that their ability to collect sufficient food is decreased still further. A second form of interference may take place amongst some visually searching birds even when no overt interactions occur. Feeding rate may be reduced because the proximity of other birds is distracting or because many birds reduce the density of available prey by driving them beneath the surface or by removing the accessible fraction faster than it is replenished (Goss-Custard 1970b, 1976), a phenomenon recently termed "resource depression" by Charnov et al. (1976). In either case, an increase in bird density could further increase the difficulties of collecting sufficient food.

CONCLUDING REMARKS

To conclude, where food shortage is already a contributory factor to winter mortality and an increase in bird density is likely to occur after part of the habitat is removed, a reduction in the feeding grounds seems likely to make an already difficult situation worse. This is because all the ways in which the birds seem likely to respond to the changed circumstances would reduce the rate at which they can feed. First, packing into the preferred feeding areas which remain, assuming that this is in any case possible, would reduce food abundance and may decrease feeding rate still further through increased interference. Second, feeding more in the less favored parts of the shore would mean that the birds would feed less profitably. Third, feeding on a wider range of size classes of prey would probably lead to a reduction in ingestion rate because the birds may already select the prey sizes which maximize the rate at which they collect food (Goss-Custard 1977c, this volume).

The reliability of this approach to making predictions about the effects of a loss of habitat on bird numbers depends a great deal on the evidence that birds already experience food shortage, and this is not easily obtained in short-term environmental impact studies. Furthermore, the degree to which food scarcity is a contributory factor to mortality is likely to vary both between estuaries, because food abundance varies considerably (Goss-Custard et al. 1977b), and between species within the same estuary. Hence each situation has to be examined in depth. One advantage of the approach is that it is unlikely that birds would be able to respond successfully to the reduction in food supplies: hungry birds would be expected to have already tried all available means of securing enough food. A disadvantage is that the approach fails to predict by how much survival and reproductive rates might be affected by a loss of feeding grounds. Furthermore, problems arise where food shortage does not occur at present. In such cases, it is necessary to predict at what point survival and reproductive rates will be affected by successive reductions in the food supplies, and whether or not birds that leave the estuary could utilize new grounds further into, or even beyond, the existing winter range of the population. Such difficulties underline the extent to which our present attempts at prediction need to be improved.

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SUMMARIZING REMARKS, PART I

JOSEPH R. JEHL, JR.[1]

Let me start by thanking Frank Pitelka for his efforts in putting this symposium together. I have enjoyed each of his papers, many of his monologues, and his several summaries.

I would also like to compliment the participants for offering such a stimulating group of contributions. Rather than rehash the papers, I want to discuss some of the major points that were raised, as well as some ideas about possible future research.

Obviously, we have come a long way recently in our studies of shorebird distribution and ecology. One very impressive point was that we are starting to get some solid data on how shorebirds utilize certain areas through an entire season. Also, up to now, most of us have looked very narrowly at habitat requirements, and we have been made aware of the importance of alternate feeding or roosting sites that may be used when the prime habitat is disturbed, flooded by fresh water, etc.

We have also learned that some species are highly philopatric and may return to the same pond or stretch of beach each winter. This, of course, has important management overtones.

We are also beginning to get a better handle on the distribution and importance of staging areas, such as Bolinas Lagoon or the northern High Plains. And is there anything to compare with the Copper River Delta and its breathtaking hordes of migrants? We are sobered to realize that there are no other areas to take its place if it is disturbed.

We do not yet have sufficient data on several topics. For example, we know very little about geographic patterns in the distribution of age and sex classes in most species, although for a few it is clear that adults and juveniles may occupy different areas in winter or may utilize different migration routes. Such patterns are so widespread in migratory passerine birds that it is surprising that they have been overlooked or unstudied in shorebirds.

We also need more thinking about the role of tradition in the establishment and maintenance of migration routes and wintering grounds. Much important work on this subject was done by Al Hochbaum years ago, and it is a subject requiring further study.

In reviewing the presentations on ecology, I think we must all be impressed with problems faced by our migratory shorebirds. Consider a bird programmed by 10,000 years of postglacial evolution to hit a specific staging area after a flight of hundreds of miles. It arrives exhausted, fat reserves nearly gone, only to find that what was a slough a few months ago is now a parking lot. And no alternate sloughs are available. I think that the data we have heard on philopatry, migratory routes, and tradition all tie into a nice package that we can use to document the need for wetlands preservation. With these data we are in an excellent position to suggest more appropriate responses to the environmental actions that confront us.

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Although our data on shorebird distribution are relatively good, they are unsophisticated. Most of the literature contributed by the amateur community has been concerned with range extensions or rarities. While such data are important in determining trends or shifts in populations, for present needs they are largely irrelevant. What we don't yet know, for example, is what percentage of the Sanderling population on the west coast of the Americas winters, say, between 40-50°N, nor do we know how wintering populations of this (or any) species are segregated by age or sex classes.

Some of these data can be derived from Christmas Counts, and the lagoon surveys such as have been conducted in California, and which should be expanded to other areas. Such data are important, because in planning for the future we might want to trade off "juvenile habitat" for that frequented by adults.

The possibility of different wintering areas of age and sex classes raises some interesting ecological questions. As you recall, Dr. Pitelka long ago advanced the view that the early departure of adult sandpipers from arctic breeding areas could be a mechanism for insuring a more abundant food supply for the chicks and remaining adults. Similarly it has also been suggested that it would be ecologically advantageous for a species to split wintering areas, with males in one area and females in another. That idea, however, is fallacious, because in species in which there is pronounced sexual size dimorphism (as in most shorebirds), the sexual segregation would only increase the frequency of similar morphs in one area, and the expected result would be to *increase* intraspecific competition. It is fun to speculate on ecological matters, but we might be better off to gather some solid distributional data first. Sometimes the world is not quite as we would like to design it.

I have been impressed by new techniques discussed today. For example, the ability to analyze castings of oystercatchers and other species means that in some cases we do not have to collect specimens to study feeding habits. And furthermore, we may now be able to study the daily or seasonal changes in foraging patterns of individuals. This technique requires a lot of hard work, and it should be encouraged.

In order to have a better understanding of shorebird movements, we need more extensive banding studies. As an example, studies in Europe have indicated that the eastern population of Curlew Sandpipers migrates to northern Africa, and molts there before continuing to wintering grounds in south Africa, whereas the Asian population completes its migration to Australia before molting. Without information on populational differences in behavior, we might arrive at erroneous conclusions about the importance of staging areas, feeding grounds, or molting localities that would defeat the purpose of any management/conservation plans.

But in some cases, as Semipalmated Sandpipers, we find there is sufficient morphological variation to distinguish local populations. Using mathematical techniques developed over the past decade, it would be possible to refine our knowledge of geographic variation in many species, and thereby study migration patterns faster, easier, and cheaper than can be done by setting up nets, ringing birds, and hoping that some will be recovered somewhere—eventually. I think such morphological studies are of great potential importance, but they are unlikely to be funded at present. Besides, they are mostly unfeasible, because they rely on series of specimens of breeding birds from several areas within a species' range. In most cases, such series are unavailable for given species even for one area, even for Barrow, where taxonomically minded California ornithologists have been studying for many years. Current collections, amassed over many years, often with no special purpose in mind, and often by persons of varying competence, are simply not adequate for these kinds of modern biological studies. Collecting the needed material would have no effect on populations, and as biologists, we should encourage (or at least not impede) such programs.

The other problem with using museum collections is that it is no easier to pull together information from collections today than it was in 1910, when Wells W. Cooke wrote his treatise on shorebird migration. We need a national retrieval system for collections so that we can take inventory of our needs and move ahead.

Finally, the most obvious overtone that has permeated the meeting so far is that everything we do will have to be evaluated in terms of "management." We are continually asked to plan on a sustained yield basis, which we seem to accept when it comes to cattle or tuna, but not to birds or marine mammals. And we are increasingly being asked to compromise—to evaluate the effects of an action and to be prepared for trade-offs.

So perhaps our greatest immediate need is not more data but what Daniel Kozlovsky has called "an evolutionary and ecological ethic"—a philosophy that gives us some guidelines in our relationship to the environment, and one that may help us live with the hard decisions that will have to be made in the near future.

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FEEDING ECOLOGY OF BLACK OYSTERCATCHERS ON SOUTH FARALLON ISLAND, CALIFORNIA

STEPHEN H. MORRELL, HARRIET R. HUBER, T. JAMES LEWIS, AND DAVID G. AINLEY[1]

ABSTRACT.—South Farallon Island, 45 km west of San Francisco and 38 hectares in size, has approximately 5.4 km of rocky coastline and supports a population of about 55 Black Oystercatchers, *Haematopus bachmani*. The diet of this species on South Farallon has been studied for the past 6 years (1971–76) by collecting and identifying the remains of food brought to nest sites for chicks (20 nests at 12 different sites), by observation of birds at occupied nests, and by observation of birds feeding in the littoral zone and on a 5-ha marine terrace 10 m above the littoral.

The oystercatchers defended territories that included the area within 20 m of nest sites and mussel beds or sections of mussel beds within sight of the nest but sometimes as far as 60 m away. These feeding territories were defended year-round but least intensely during winter. When hatching year oystercatchers reach independence they may still forage occasionally in their parents' territory. However, the adults often chase them away. During fall and winter, 20 to 30 or more oystercatchers congregate at a gently sloping mussel bed and adjacent supralittoral marine terrace on the southwest side of the island. Most of these birds are probably nonbreeders, including hatching year birds, since other areas of the island we are able to see are essentially occupied continuously by the birds that breed there.

Diet is apparently determined by prey availability within the defended territory, and to a lesser extent by distinct preferences for certain prey at certain times. Based on analysis of invertebrate remains for pairs at specific nest sites for several years, at least part of the diet appears to remain constant from one year to the next. Prey availability is in turn determined by topography of the shoreline–sloping shoreline supports beds of the California mussel, *Mytilus californianus*, while steep shoreline lacks mussel beds. Both types of shoreline support limpet populations, mainly *Collisella scabra*, *C. pelta*, *C. digitalis*, and *Lottia gigantia*. At nests where mussels comprise 40% or more of the prey remains (14 of 20 nests), the diet, as indicated by prey remains identified, is more varied (9 of the 14 nests had 5 or more other prey species) than at nests where mussels comprise 30% or less of the diet (6 of 20 nests; 2 of the 6 had 5 or more other prey species). This probably reflects the diversity of prey available in mussel beds. For example, the crab *Oedignathus inermis* is usually found sublittorally. However, when in the littoral zone, *Oedignathus* is found in association with mussels. *Oedignathus inermis* was not found at any of the 6 nests with 30% or less mussels, but it was found at 8 of the 14 nests with 40% or more mussels. On the other hand, mussels, when available, are taken in preference to limpets as food for chicks. The reason for this may be that if larger mussels are brought back, fewer trips have to be made.

Continuous dawn-to-dark watches were conducted on 8 days during the 1976 breeding season, one of three different nests being watched each day. Chicks were 1 to 40 days of age. Prey that would not be detected as remains at the nest site (nemertean and polychaete worms and tenebrionid beetle larvae) comprised up to 57% (by number) of the food items brought to chicks. The beetle larvae represented 30% of the chicks' diet on three of the eight days. Those larvae are captured in the soil of the marine terrace, where their availability apparently fluctuates with soil moisture, the larvae burrowing deeper into the soil as the surface becomes dry.

Four additional continuous watches of chicks old enough (67–100 days) to forage with their parents in the littoral zone revealed that limpets were the major prey item (60–85%), whether fed to a chick by a parent or captured by the chick itself. Mussels, all of which were opened by a parent, were a distant second (16% or less), and nemertean and polychaete worms comprised less than 3% of the diet. During these four watches, 5–24% of the prey items could not be identified.

The diet of newly independent chicks is mainly limpets, littoral worms, and supralittoral beetle larvae. The skill required to open mussels is apparently not sufficiently developed when the chicks first become independent. They thus do not forage heavily on those bivalves at first. Attempts are now being made to determine the age at which this aspect of feeding becomes possible.

Observations made on oystercatchers over a period of 13 months revealed that the phase of the

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tidal cycle greatly affects their activity in the littoral zone. Feeding comprises 35% of all activity during the low half of the cycle and only 9% during the high half of the cycle. Considering feeding activity alone, 70–95% is done during the low half of the cycle, depending on swell height and exposure of different areas to swells. The feeding activity observed on the high half of the tide cycle occurs mostly in late summer when adults are feeding large, rapidly growing chicks and in fall when fledglings require more time to feed themselves as they perfect their foraging skills.

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SEASONALITY OF SUMMER HABITAT AND SOCIAL SYSTEM OF RED PHALAROPES

DOUGLAS SCHAMEL AND DIANE TRACY[1]

ABSTRACT.—Polyandry has long been suspected in phalaropes. Conclusive evidence has only recently been given for one species, the Northern Phalarope (*Phalaropus lobatus*). In this paper, we present the first evidence for polyandry in the Red Phalarope (*Phalaropus fulicarius*). This phenomenon has never been documented in the Wilson's Phalarope (*Phalaropus tricolor*). Polyandry, in general, seems to be found where males assist with incubation, excess males are available in the population, and sufficient food resources can be mobilized to produce multiple clutches. This is also true for phalaropes. Intensive banding studies at Barrow, Alaska, indicate that only a small percentage of the population is site-faithful. Phalaropes are apparently not "bound" to a nesting area and are thus free to seek out the most productive areas for breeding.

[Ed. note: This paper has been published under the title "Polyandry, Replacement Clutches, and Site Tenacity in the Red Phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. Bird-Banding, 48:314–324, 1977.]

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AVAILABILITY AND UTILIZATION OF INVERTEBRATES AS SHOREBIRD FOOD ON A HUMBOLDT BAY MUDFLAT

L. F. CARRIN, N. D. HOLMBERG, AND S. W. HARRIS[1]

ABSTRACT.—Monthly core samples were taken from the upper 15 cm of a Humboldt Bay mudflat, northern California, between August 1970 and August 1971. Field observations and net sweeps in residual tide pools, channels, and on incoming tides provided additional data. Invertebrate populations were higher in the mud core samples than in the overlying water. Within the mud profile, 93.5 percent of the individuals and 60 percent of the total biomass were contained in the top 5 cm. The most abundant species were *Leptochelia dubia* (a cheliferan), *Transennella tantilla* (a small clam), *Notomastus tenuis* (a polychaete), and amphipods. More invertebrates occurred in summer than winter. Examination of 7 species of shorebirds shot while feeding on the study area revealed that, within broad limits, they fed mainly on expected items when behavioral and morphological characteristics of the birds were considered.

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FLOCKING BEHAVIOR IN WINTERING DUNLIN

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ABSTRACT.—This study was undertaken to describe the how of flock structure and movement, hopefully to provide insight into the why of it. Using color-banded birds, positioning and association of individuals were measured. Relative to immatures, adults occurred less often in areas postulated as having a high degree of exposure to avian predation. The social structure was anonymous, with no evidence found of maintained associations between individuals. Movement was based on flushing behavior of and within flocks. Two basic types were defined, uniform flush (continuous propagation) and single point flush (noncontinuous propagation). Measurement of the origin and directions of each flush type in relation to defined positions within flock structure and of their effect on flock density and flight behavior revealed uniform flush to be centripetally based causing coalescing of individuals while single point flush acted centrifugally to cause dispersal. Further correlation revealed initiation and speed of propagation to uniform flush to be directly related to the degree of exposure to avian predation. From this, uniform flush is postulated as being a response to real or imagined danger. From cited literature, single point flush is postulated as being a response to increased food availability. Concept of bonds between birds maintained by visual and acoustic perception is used to discuss the social tendency in Dunlin. Within this framework, elements of uniform flush are shown to strengthen bondage and thereby increase flocking tendencies. Single point flush in contrast acts to weaken bondage and thereby cause the breakdown of flocks. Conclusion is drawn that the evolutionary cause of flocking in Dunlin is predation.

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BIOLOGY OF SHOREBIRDS SUMMERING ON ENEWETAK ATOLL

OSCAR W. JOHNSON[1]

ABSTRACT—Golden Plovers, Whimbrels, Bristle-thighed Curlews, Wandering Tattlers, and Ruddy Turnstones were studied at Enewetak Atoll, Marshall Islands, during the summers of 1970 and 1973. These birds are representative of an unusual behavioral feature in shorebirds wherein many nonbreeding individuals remain on wintering areas during the boreal summer. Most appear to be first-year birds lacking the physiological stimulus for migration.

Plovers and turnstones were particularly abundant with flocks of 20 or more relatively common. Feeding activity coincided with low tides, and occurred mostly on the reef-flat along the seaward margin of the atoll. Upland sites were frequented during periods of high tide.

Testes were histologically immature except for very limited sperm production in some Whimbrels and curlews. No recrudescence of ovaries was found. Despite the lack of gonadal activity, a few individuals achieved breeding coloration. Most birds had either a partial breeding or nonbreeding plumage. The sex ratio of plovers was strongly biased toward males (about 5:1), and apparently balanced in the other species.

Golden Plovers had molted their juvenal remiges during the winter, and were well into a complete prebasic II molt by mid-July. Whimbrels and Bristle-thighed Curlews molt juvenal remiges in the spring and early summer, and were nearing completion of alternate I development in mid-July. Wandering Tattlers were replacing juvenal primaries in early summer with molt commencing from a central locus; this unusual pattern of primary molt appears to be age-related, occurring only in first-year birds. Ruddy Turnstones had no recent and/or ongoing remex molt. Evidently young birds retain juvenal wing feathers through their second summer of life. In all species studied, the development of alternate feathering was frequently very slight such that the individual would essentially pass from one basic plumage to another while on the winter range.

Fat content in summering birds varied from around 3 to 6 percent of body weight, restricting them to relatively short flights. Flight range predictions were much too conservative when calculated according to formulae based upon aerodynamic theory. Possibly the streamlined body-form of shorebirds results in greater flight efficiency than heretofore recognized in studies of avian aerodynamics.

Shorebirds display an unusual behavioral feature wherein substantial numbers of nonbreeding birds remain on wintering grounds during the boreal summer. This pattern is particularly common in long-distance transequatorial migrants. The biological basis for this phenomenon is unknown, although it appears that these are mostly first-year birds which perhaps lack the physiological stimulus or capacity for migration. Literature pertaining to migratory arrest and its possible causative factors was reviewed by McNeil (1970) and Johnson (1973).

Most of this paper will concern reproductive condition, plumage, molt, fat content, and flight range in five species of shorebirds occupying a central Pacific wintering area during midsummer. Surprisingly little is known about such features in shorebirds for this phase of their life cycles. Major portions of the material upon which this treatment is based have been published elsewhere (Johnson 1973, Johnson and Morton 1976, Johnson 1977).

MATERIALS AND METHODS

Fieldwork was conducted at Enewetak Atoll in the northwest Marshall Islands (approximately 11°N, 162°E) from 9 June through 6 July 1970; and from 4 July through 17 July 1973. The frequently used spelling "Eniwetok" represents a distortion of the native "Enewetak" which occurred during World War II and the subsequent nuclear testing period. Observations and collections were made on Aomon, Biijiri, Chinimi, Enewetak, and Rojoa islets. The following species were studied: American

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FIGURE 1. Much of the land surface at Enewetak is covered by shrubby vegetation. The predominant plants in this photograph are *Scaevola taccada* and *Ipomea tuba*.

Golden Plover (*Pluvialis dominica fulva*), Whimbrel (*Numenius phaeopus*), Bristle-thighed Curlew (*N. tahitiensis*), Wandering Tattler (*Heteroscelus incanus*), and Ruddy Turnstone (*Arenaria interpres*).

Laboratory and field techniques are detailed in other publications (Johnson 1973, Johnson and Morton 1976, Johnson 1977). Basically, procedures involved: (1) various surveys and counts of shorebirds on the atoll; (2) morphological and histological examination of gonads; (3) plumage evaluations (using flat skins) based upon fading, wear, and molt of the flight and body feathers; (4) ether extraction of lipids from preserved carcasses.

RESULTS AND DISCUSSION

THE ATOLL ENVIRONMENT

Enewetak is representative of the multitude of Micronesian atolls which collectively form an important component of wintering habitat for many shorebirds. The atoll consists of some 40 small coral islets surrounding a lagoon approximately 20 nautical miles in diameter. Substantial ecological disturbance occurred during World War II and as a result of extensive nuclear testing over the period from 1948 to 1958. Pertinent summaries of modern man's impact upon the biota of Enewetak have been published by Woodbury (1962) , Jackson (1969), and Fall et al. (1971). On many of the islets, vegetative recovery over the past two decades has produced an extensive shrub cover (mostly *Scaevola taccada* and *Messerschmidia argentea*) interspersed with open areas dominated by various grasses and forbs (Fig. 1). Present habitats are possibly more attractive to shorebirds than the more heavily vegetated predisturbance situation.

Migratory routes of shorebirds as they traverse the Pacific are not well understood. Baker (1951) postulated three major migration corridors (Fig. 2). With the exception of the Whimbrel, many of the shorebirds occurring at Enewetak probably utilize the "Nearctic-Hawaiian" route. There are only three unconfirmed

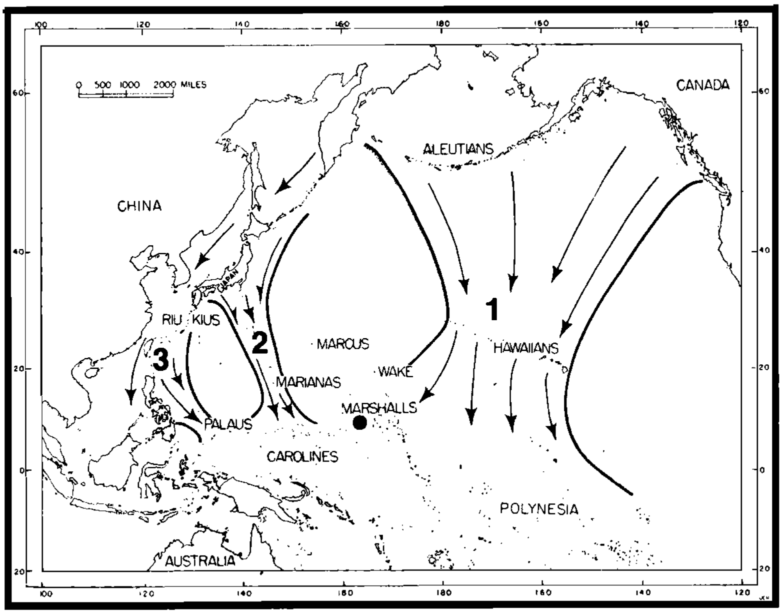

FIGURE 2. The three major migratory corridors for shorebirds in the Pacific as proposed by Baker. Corridor 1 is the "Nearctic-Hawaiian" route which probably is the most important flyway relative to Enewetak (approximate location indicated by black dot). Corridors 2 and 3 are the "Japanese-Marianan" and "Asiatic-Palauan" flyways, respectively. (From Baker 1951, with permission.)

sight records of Whimbrels in the Hawaiian area (Ely and Clapp 1973), hence their presence in Micronesia evidently occurs via eastward movements from the Asian coast and adjacent island groups (Fig. 2).

SHOREBIRD ABUNDANCE AND BEHAVIOR

Golden Plovers and Ruddy Turnstones are the most abundant shorebirds present on Enewetak during the summer with flocks of 20 or more seen commonly. Similar findings were noted by Carpenter et al. (1968) in records gathered during portions of four boreal summers spent at Enewetak. Census information is limited, and the available data are shown in Table 1. Carpenter et al. (1968) present figures for the entire atoll. However, they do not describe methods, and the accuracy of their data is difficult to assess. During my visits, it was unfeasible to survey the whole area and counting was restricted mainly to Enewetak islet.

My data in Table 1 show daily fluctuations in abundance which reflect movements of birds between adjacent islets. Plovers, for example, were sometimes absent from Enewetak islet on a given day (or portion thereof) only to reappear later. Movements appeared keyed to certain particularly desirable habitats. In 1973, an excavation (part of an ERDA project called "EXPOE") on Aomon islet produced a relatively large flat area with a freshwater pond in its center. Flocks of shorebirds congregated there (especially during periods of high tides and in the evening) with at least 100 plovers present on one occasion (Table 1). The airstrip on Enewetak islet is another attractive site, and is used extensively by plovers and turnstones. The birds loaf on the pavement, utilize freshwater puddles, and (based upon behavioral observations) appear to capture insects in grassy areas

TABLE 1
POPULATION ESTIMATES OF SUMMERING SHOREBIRDS ON ENEWETAK

Species	1966[a]	1967[a]	1970[b]	1973[b]	
Golden Plover	183	139	0–35	10–30	20–100
Whimbrel	no data	no data	0–6	1–6	0
Bristle-thighed Curlew	50	18	0–1	0	3–10
Wandering Tattler	22	24	0–12	0–4	0
Ruddy Turnstone	129	102	0–30	0–9	12–20

[a] Data for these years are from Carpenter et al. (1968), and represent total surveys of the atoll with helicopter assistance.

[b] Data for these years are those of Johnson, some of which have been published (Johnson 1973). The 1970 data represent 14 census counts on Enewetak islet only, conducted from 9 June through 6 July. Data for 1973 are respectively: first column, 5 counts on Enewetak islet from 4 July through 17 July; second column, 2 counts on Aomon islet, 10 and 15 July. Values of "0" represent daily fluctuations at a particular site, and reflect intra-atoll movements of birds.

along the runway aprons. Intra-atoll movements of highly mobile shorebirds make it very difficult to obtain accurate estimates of total populations. My observations on only two islets of the forty making up the atoll would imply that the Carpenter et al. (1968) figures are too conservative. On the other hand, habitat conditions on the islets which I surveyed perhaps attracted disproportionately large numbers of birds; also population levels might fluctuate from one year to another.

During periods of low tide, birds leave upland sites and feed in the intertidal zone. Feeding was confined almost exclusively to the seaward margin of the atoll with birds seen only infrequently on the lagoon side. An extensive and productive reef-flat community (Odum and Odum 1955) accounts for the attractiveness of the seaward zone to feeding shorebirds (Fig. 3). In contrast to plovers and turnstones which commonly frequented upland sites, Whimbrels, curlews, and tattlers behaved differently. The latter species were encountered almost exclusively on beach and intertidal habitats. Bristle-thighed Curlews were infrequent on Enewetak islet, but relatively common on various of the other islets. Possibly, this species is particularly intolerant of human activity (which is substantial on Enewetak islet) and prefers relatively undisturbed sites.

SEX RATIOS AND REPRODUCTIVE CONDITION

Van Oordt (1928) found that summering populations of Knots (*Calidris canutus*) and Ruddy Turnstones in Holland contained a preponderance of males. A similar disparity occurs at Enewetak, but thus far it is apparent only among Golden Plovers. The combined tally by species and sex for all birds collected in 1970 and 1973 is: Golden Plover, 25 males and 6 females; Whimbrel, 2 males and 4 females; Bristle-thighed Curlew, 3 males and 5 females; Wandering Tattler, 4 males and 7 females; Ruddy Turnstone, 13 males and 9 females. It is reasonable to assume that the foregoing reflects random sampling since birds were collected opportunistically. The significance of the distorted sex ratio in plovers is unknown. Perhaps females are more likely to achieve sexual maturity and return to breeding areas in their first year, or possibly there is differential movement of the two sexes on the wintering grounds resulting in geographic separation.

In almost all males, the testes were small and inactive. No sperm were being produced in any of the plovers, tattlers, or turnstones collected (Table 2). In one of two Whimbrels, and one of three curlews examined, testicular development had proceeded to the extent that a few spermatozoa were present. It is doubtful

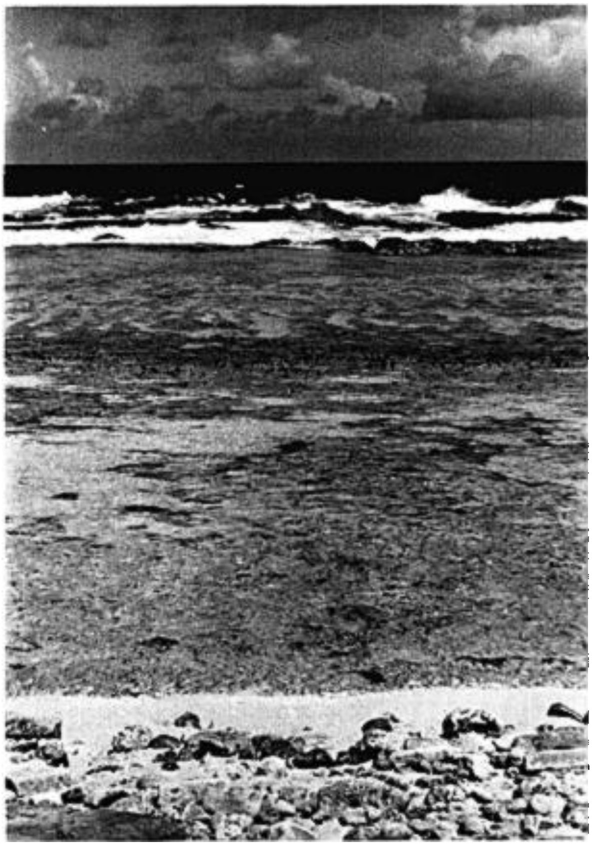

FIGURE 3. A biologically diverse and productive reef-flat occurs along the seaward margin at Enewetak. In some areas it is much wider than in this photograph. Shorebirds fed extensively on such habitat during low tides.

TABLE 2
SUMMARY OF REPRODUCTIVE ORGAN DEVELOPMENT[a]

Species (N)	Range in wt. both testes (mg)	Sperm production	Range in ovary wt. (mg)	Range in dia. largest follicles (mm)	Egg production	Range in oviduct wt. (mg)
Golden Plover (23♂, 6♀)	5–40	no	29–80	1.4–2.0	no	13–71
Whimbrel (2♂, 3♀)	23–45	limited	63–102	1.3–1.5	no	66–77
Bristle-thighed Curlew (3♂, 5♀)	10–63	limited	45–66	1.1–1.4	no	71–111
Wandering Tattler (2♂, 6♀)	4–6	no	33–79	0.9–1.8	no	13–38
Ruddy Turnstone (11♂, 7♀)	2–27	no	22–64	1.1–1.6	no	16–19

[a] The table is a composite of both published (Johnson 1973) and unpublished data.

FIGURE 4. Variations in the plumage of Golden Plovers summering on Enewetak. The bird on the left showed partial alternate development with scattered black feathers on the cheeks, throat, and breast; plus a fairly distinct white stripe over the eye and down the side of the neck. The other specimen displayed alternate feathering. (From Johnson 1973.)

that either individual would have been fertile since sperm production was very low. The ultimate degree of testicular recrudescence among summering shorebirds is unknown; however, based upon collection dates (early to midsummer) further maturation seems unlikely. Additional details on testicular histology are given elsewhere (Johnson 1973).

Although van Oordt (1928, 1931) postulated a direct relationship between extent of development of the testes and type of plumage in summering shorebirds, my data do not fully support this correlation. Variations occurred in testis weight (Table 2), with larger testes displaying at least partial activation of the seminif-

TABLE 3
SUMMARY OF PLUMAGE AND MOLT[a]

Species	Remiges	Rectrices	Body molt	Overall appearance[b]
Golden Plover	Vary from unworn to moderately worn basic I feathers; prebasic II molting through primary 6 in some birds; secondary molt commences with loss of primary 6.	Replaced in most birds during prebasic I molt; molting commences with loss of primary 5 or 6.	Extensive in most birds.	A, P, B; undergoing prebasic II molt.
Whimbrel and Bristle-thighed Curlew	Prebasic I molt recently completed or nearing completion.	Erratic pattern of prebasic I molting, some juvenal feathers retained; no molt occurring.	Slight	P, B
Wandering Tattler	Prebasic I molt underway; unusual pattern of primary loss commencing of a central locus.	Erratic pattern of prebasic I molting, molt underway in 2 of 3 specimens.	Slight	B
Ruddy Turnstone	Basic I in probable 2nd-year birds, juvenal in 1st-year birds; no molt occurring in either group.	As with rectrices	Slight	A, P, B

[a] Data from Johnson (1977) represent birds collected during the period from 4 through 17 July 1973.

[b] A = alternate (bright reproductive coloration); P = partial alternate (moderate reproductive coloration); B = basic (no reproductive coloration). The variation reflects individual differences in the extent to which alternate body feathering is acquired in the late winter and spring. Birds considered "basic" have so few alternate feathers that they essentially molt from one basic plumage to another.

erous epithelium (i.e. increased numbers of primary spermatocytes in synapsis). This modest recrudescence implies elevated levels of gonadotropins in the blood, and perhaps also the secretion of testicular androgens. Nonetheless, birds with larger testes were often in a drab nonbreeding plumage.

All females collected at Enewetak had small and inactive reproductive organs (Table 2). Similar findings were reported in several species of summering shorebirds by van Oordt (1928, 1931) and Loftin (1962). Further information on my specimens is available elsewhere (Johnson 1973).

PLUMAGE AND MOLT

General features of plumage development in each species are summarized in Table 3. A more detailed treatment was published by Johnson (1977), and only major findings will be discussed in this paper.

The plumage of each individual was a composite of old and new feather generations, with the result that birds varied conspicuously in appearance. Some had predominantly new plumage with resultant bright coloration and vice versa (Figs. 4, 5). In many birds, the development of alternate feathering is so slight that the

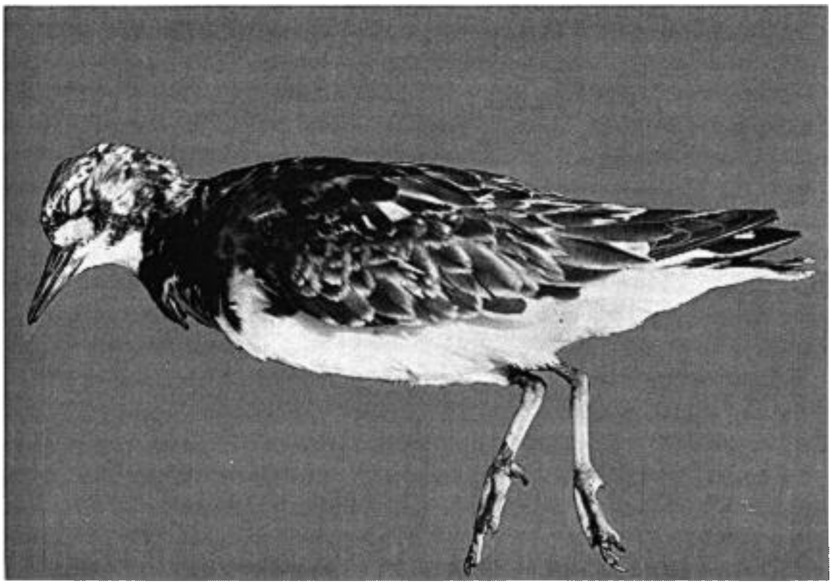

FIGURE 5. Partial alternate feathering was relatively common among Ruddy Turnstones at Enewetak. Such individuals had scattered chestnut-colored feathers dorsally, and a faint harlequin face pattern. (From Johnson 1973.)

individuals essentially remain in basic plumage during the summer period. At Enewetak, basic and partial alternate plumages are much more common than alternate in flocks of summering birds. Golden Plovers were particularly easy to observe, and our counts of various flocks (generally 20–30 birds per flock) indicated alternate plumage in only about 10 percent of the individuals seen.

The remainder of this section will describe pertinent findings in each of the species studied.

Golden Plovers varied in relative wear of flight feathers. In some, the primaries were bright brown-black in color and unworn; in others, there was moderate fading and wear (Fig. 6). If some first-year birds molt their primaries during the winter and others do not, then moderately worn feathers should represent the juvenal plumage. However, these feathers were not nearly so worn as definite juvenal primaries in the other species studied (Fig. 7). Hence, it appears that all first-year plovers replace their juvenal remiges when they molt into basic I plumage during the winter. The degree of wear would then relate to at least two factors—the chronology of molting and the extent to which birds move on the winter range subsequent to molt. Substantial individual variation as to the onset and rate of primary molt has been described in Golden Plovers and other shorebirds (Middlemiss 1961, Johnston and McFarlane 1967, Thomas and Dartnall 1971a, b, Pearson 1974, Dare and Mercer 1974, Evans 1975, Elliott et al. 1976). It is likely that the Golden Plover population at Enewetak in early summer represents a composite with some birds perhaps resident since fall migration and others arriving after flying varying distances during the winter and spring. Differences in primary wear would thus be an interaction between two variables—when the feathers were acquired and the subsequent mileage placed upon them.

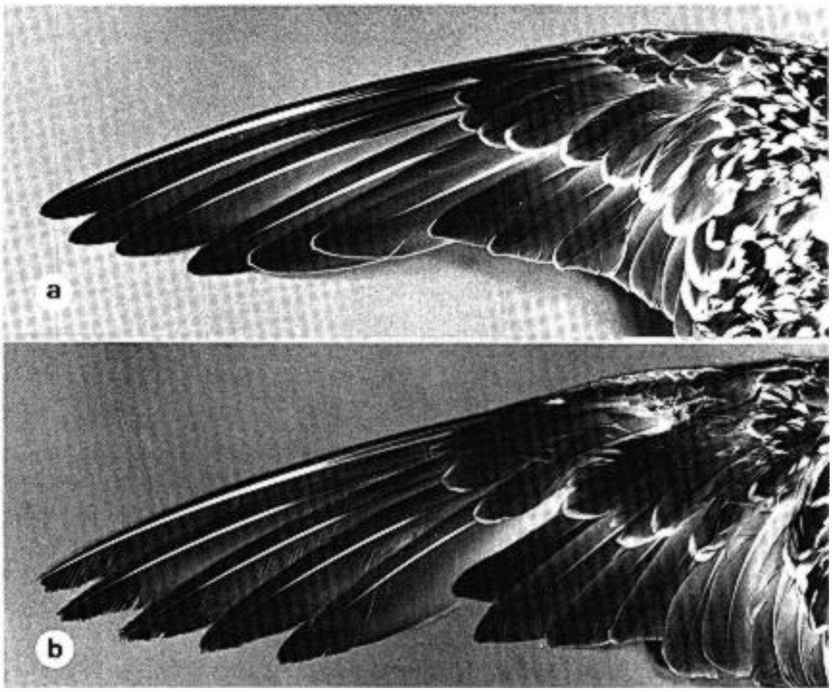

FIGURE 6. Wings from Golden Plovers collected in early July at Enewetak. (a) Primaries 1–4 are new (4 is short and hidden from view); primaries 5–10 represent an unfaded and unworn feather generation that is being replaced. (b) Primaries 1–5 are new (5 is short and hidden from view); primaries 6–10 are moderately worn and faded, but not to the degree characteristic of juvenal feathers. Hence, the same feather generation is being replaced in each specimen. The wings shown represent the extremes in the range from unworn to moderately worn primaries. All other plovers examined fell within the limits illustrated here. (From Johnson 1977.)

Plovers throughout the gradient of feather wear (Fig. 6) were molting their primaries. Some had progressed as far as primary 6. There was also extensive body molt in progress, hence the birds were undergoing a complete prebasic II molt in early summer. This appears to be out of synchrony with the molt schedule of plovers on the northern breeding grounds.

Whimbrels and Bristle-thighed Curlews molt their juvenal primaries in the spring to early summer period. Most of the birds examined had completed wing molt; two individuals were still molting extremely worn juvenal primaries when collected on 6 and 15 July 1973, respectively. In contrast to the plovers, these species would have a later prebasic II body molt which may in fact be chronologically similar to corresponding prebasic molting in postnuptial adults. Body molt was slight, and the birds were nearing completion of alternate I plumage development. The latter varies among individuals as to the number of more brightly colored alternate feathers in the overall plumage (Table 3).

Wandering Tattlers were molting juvenal remiges in July. The pattern of primary molt is unusual in that it commences centrally with primary 6, then proceeds distally to primary 10 (Fig. 7). Following the loss of primary 10, my small sample of specimens molted sequentially primaries 1, 5, and 4; I was unable to trace

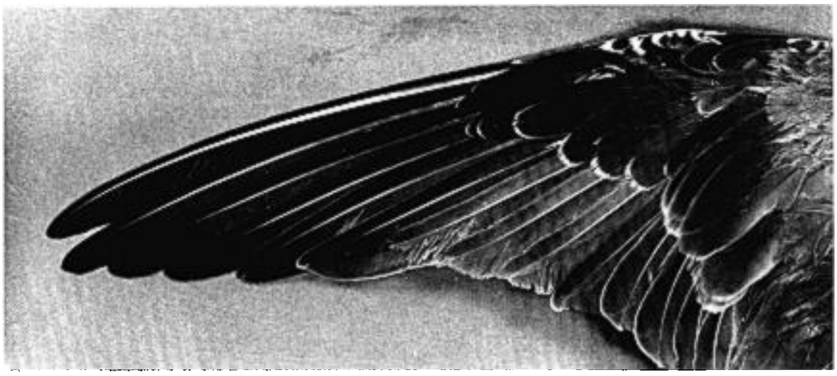

FIGURE 7. Wing from a Wandering Tattler collected in mid-July at Enewetak. Primaries 2, 3, and 4 are worn, faded juvenal feathers which typify the appearance of similar feathers in Whimbrels, curlews, and turnstones. The pattern of primary replacement is unusual in tattlers since it commences with feather 6. (From Johnson 1977.)

events further with the materials available. In contrast to the above, museum skins of Wandering Tattlers often show the typical shorebird sequential molt pattern commencing with primary 1. Comparable findings were reported in Wandering Tattlers and Polynesian Tattlers (*Heteroscelus brevipes*) by Prater and Marchant (1975), and in several other species of shorebirds by Pearson (1974) and Elliott et al. (1976). Each of these investigators concluded that the variation is age-related with central locus molting restricted to first-year birds.

Tattlers had fewer alternate feathers than any of the other species examined (Table 3). Hence, the alternate I condition in these birds involves a very drab plumage consisting mainly of worn basic feathers and probably some juvenal feathers as well.

Ruddy Turnstone specimens were divisible into definite first-year and probable second-year age-groups (see Acknowledgments). First-year birds had retained their juvenal remiges, while in second-year birds these feathers were referable to the basic I plumage. Neither group showed any recent and/or ongoing remex molt. Evidently, first-year birds utilize juvenal wing feathers through their second summer of life. This pattern is comparable to those shorebirds which are short-distance migrants, and which typically replace their juvenal remiges during the prebasic II molt (Witherby et al. 1940, Palmer 1967, Pearson 1974). The data suggest that the timing of subsequent prebasic molt in summering turnstones might coincide with that of postnuptial adults.

Overall feathering in turnstones (Table 3) was distributed as follows relative to the two age-groups: first-year, 2 partial alternate and 1 basic; second-year, 2 partial alternate and 1 alternate.

FAT AND FLIGHT RANGE

Fat cyclicity has not been examined widely in shorebirds. The primary studies are those of Johnston and McFarlane (1967) on Golden Plovers at Wake Island in the Pacific; McNeil (1969, 1970) and McNeil and Cadieux (1972a, b) on various charadriids and scolopacids in the Gulf of St. Lawrence and in northeastern Venezuela; Page and Middleton (1972) on Semipalmated Sandpipers (*Ereunetes*

TABLE 4

FAT CONTENT OF SUMMERING SHOREBIRDS[a]

Species (N)	Body wt. (g)[b]	Ether-extractable fat (g)[b]	Fat content as % of body wt.[b]
Golden Plover (17)	116.9 (102.5–129.8)	3.4 (1.9– 5.5)	3.0 (1.7– 4.6)
Whimbrel (2)	401.2 (384.5–418.0)	23.9 (22.1–25.8)	6.0 (5.3– 6.7)
Bristle-thighed Curlew (7)	493.9 (383.0–585.0)	33.6 (12.7–63.1)	6.6 (3.3–10.8)
Wandering Tattler (3)	115.8 (96.5–132.5)	3.6 (2.5– 4.3)	3.0 (2.6– 3.6)
Ruddy Turnstone (6)	97.1 (89.1–108.0)	3.9 (2.8– 4.7)	4.0 (2.9– 4.7)

[a] Data from Johnson and Morton (1976) represent birds collected during the period from 4 through 17 July 1973.

[b] Figures represent mean and range.

pusillus) at Long Point, Ontario; and Baker (1975) on Pied Oystercatchers (*Haematopus ostralegus finschi*) in New Zealand. Only the Venezuela research provides substantial data for birds summering on their wintering grounds. To my knowledge, the information presented below (and in part elsewhere, Johnson and Morton 1976) is the first consideration of lipids in shorebirds summering on a Pacific winter range.

The data are summarized in Table 4. Fat levels varied from 3.0 to 6.6 percent of body weight. In contrast, premigratory or intramigratory fat in shorebirds ranges from around 17 to 50 percent of body weight (Johnston and McFarlane 1967, McNeil 1970, Page and Middleton 1972). The slightly higher levels of fat in Whimbrels and curlews (Table 4) may relate to their molt status (nearing completion of prealternate molt), as described earlier.

Flight range estimates for the species examined are given in Table 5. The data shown represent the leanest compared to the fattest bird in each species. Calculations appearing in the first column of range estimates ("A" in Table 5) interrelate speed of flight and energy stores to the rate of energy use during flight. Such estimates are inherently crude since flight speed is essentially a "guess" and other variables (effects of wind, etc.) cannot be delimited. Presumably, relatively fat Whimbrels and curlews were capable of sustained flights of about 600 to 800 miles with flight ranges in the other species substantially less (Table 5).

TABLE 5

APPROXIMATE CAPACITY FOR SUSTAINED FLIGHT

Species	Body wt. (g) and ether-extractable fat (g)[a]	Flight speed (mph)[b]	Flight range (miles)[c]	
			A	B
Golden Plover	108.8 (1.9), 119.5 (5.5)	65	160–430	80–200
Whimbrel	418.0 (22.1), 384.5 (25.8)	45	470–590	190–260
Bristle-thighed Curlew	383.0 (12.7), 585.0 (63.1)	35	225–820	125–455
Wandering Tattler	96.5 (2.5), 118.5 (4.3)	45	160–235	100–150
Ruddy Turnstone	97.5 (2.8), 90.0 (4.2)	40	155–250	120–200

[a] Data from Johnson and Morton (1976) represent birds collected during the period from 4 through 17 July 1973. For each species, the figures show the two specimens with minimum-maximum flight ranges, respectively.

[b] Flight speed estimates from several sources where literature summaries of such data and/or direct speed measurements are given: Cooke (1933), Meinertzhagen (1955), Johnston and McFarlane (1967), McNeil (1970).

[c] For column A, the formula used by McNeil (1969, 1970), McNeil and Cadieux (1972 a, b) and Baker (1975) was used to calculate flight range: FR = flight range in miles = $F \times S \times 9.1$ kcal/FM; where F is weight of fat in grams; S is flight speed in miles per hour; 9.1 is the caloric value of 1 gram of fat (Johnston 1970); and FM is flight metabolism. The latter is estimated by the equation of Raveling and LeFebvre (1967): $\log FM = \log 37.152 + 0.744 \log W \pm 0.074$, where W is body weight in kilograms.

For column B, the formulae and tables given by Pennycuick (1975, pp. 25–28) were used in the calculations.

All birds would have been restricted to "island-hopping" in Micronesia with no physiological potential for long-distance migration.

Range estimates in the second column ("B" in Table 5) are calculations derived from Pennycuick's (1975) formulae. The latter rest upon aerodynamic principles which avoid the questionable variables mentioned above. Results indicate considerable disagreement between the two approaches with the Pennycuick approach predicting shorter flight ranges (Table 5).

The discrepancy was greater than anticipated, and as a further test I applied both methods to data on Golden Plovers provided by Johnston and McFarlane (1967). One can select values from their paper representative of fat content in birds about to depart Wake Island northbound for the Aleutians. Here we have a known event about to occur—namely a 2400-mile flight, and the necessary variables to fit the formulae. Assuming that the fattest birds collected by Johnston and McFarlane were ready to migrate and that all fat would be burned as fuel, formula "A" predicts flight ranges of about 2800–4650 miles and formula "B" about 1250–2100 miles. It is most unlikely that all fat would be utilized during the flight. In fact, Johnston and McFarlane found that southbound plovers still contained substantial stores of lipids upon arrival at Wake Island in August.

Since formula "B" predicts that the birds would fail to reach the Aleutians, Pennycuick's approach as applied in this particular instance is much too conservative. The application of aeronautical concepts to birds obviously needs refinement, and my purpose in reporting these findings is cautionary rather than critical. Pennycuick (pers. comm.) feels that body shape and its relationship to surface drag may explain the discrepancy between actual and predicted flight range in Golden Plovers. The extent to which notable avian streamlining (as in shorebirds) reduces drag has not been studied adequately. In any event, shorebird flight appears to be highly efficient and at variance with present concepts of avian aerodynamics.

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WINTER ECOLOGY OF A BLACK OYSTERCATCHER POPULATION

E. B. HARTWICK AND W. BLAYLOCK[1]

ABSTRACT.—The movements and foraging of Black Oystercatchers were studied during winter. Many birds concentrated in mudflats during daytime where they fed on mussels (*Mytilus edulis*). The birds ignored other potential prey but had little impact on the mussel beds. More time was spent foraging in beds with higher densities of mussels and this behavior is discussed in relation to a model of optimal foraging.

Oystercatchers (*Haematopus* sp.) are shorebirds inhabiting most continental sea coasts. They have attracted considerable attention in Europe where they concentrate in large numbers on intertidal flats during winter and pose a significant threat to the cockle fishery (Hancock 1970). The birds feed preferentially on second-winter cockles (*Cardium edule*) just before they reach the size of entering the fishery (Franklin 1972). A single bird concentrating on cockles may remove over three hundred per day (Davidson 1968). The birds feed on mussels (*Mytilus edulis*) as well, and will prey on *Macoma baltica* or other bivales when cockles or mussels are in poor supply (Hancock 1970). According to Dare (1966), oystercatchers tend to concentrate in areas where cockles and mussels occur in sufficient density to sustain the relatively high daily food requirements of the birds. Heppleston (1971a) found that British oystercatchers (*H. ostralegus occidentalis*) were unable to obtain their food requirements from estuarine habitats during winter in spite of extending their foraging time into the night. These birds apparently made up their deficit by feeding at high tide on earthworms in grass fields. In a study of the anatomy of the bill, Heppleston (1970) found many sensory corpuscles which would allow the bird to probe mud or soil for invertebrates. An interesting increase in the use of terrestrial habitats by oystercatchers for feeding and also for breeding has been observed in Britain and New Zealand (Heppleston 1971a, Baker 1974). Nevertheless, the major prey items in the diet of oystercatchers are molluscs and this specialized feeding habit greatly reduced interspecific competition with other waders (Heppleston 1970). A variety of studies has been carried out on the abilities of oystercatchers to open bivalves, especially mussels (Drinnan 1958, Norton-Griffiths 1967, Heppleston 1971b). Norton-Griffiths found that some oystercatchers stabbed mussels when they were submerged and gaping while others hammered the shells open. Studies in New Zealand have indicated other differences occurring in the birds including variations in habitat selection, niche utilization, and breeding biology (Baker 1974). For example, South Island Pied Oystercatchers (*H. o. finschi*) concentrate in large flocks in habitats with soft substrates, such as mudflats. In contrast, the black phase of the Variable Oystercatchers (*H. unicolor*) occurs in smaller flocks along rocky shores. According to Baker, these are generally excluded from mudflats through competition with the South Island Pied form.

On the west coast of North America, a black form of oystercatcher occurs in relatively low numbers along the exposed coast. The Black Oystercatcher is usually regarded as a separate species, *H. bachmani,* although Heppleston (1973)

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has reviewed the systematics of the family Haematopodidae and suggests that the west coast species be regarded as a subspecies, *H. ostralegus bachmani*. However, as he points out, the classification of oystercatchers is a subject of continuing controversy and further studies are required.

Information on the biology of Black Oystercatchers was collected by Webster (1941) and more recently by Hartwick (1974). Studies to date have centered on the behavior and ecology of these birds during the summer breeding season. Their diet at that time consists mainly of mussels (*M. californianus*) and limpets (*Collisella* sp. and *Notoacmea* sp.) although other items such as polychaetes (*Nereis*) and various arthropods are also taken (Hartwick 1976). They inhabit rocky shores although occasionally pairs are seen on sandy beaches. Relatively little information exists on the ecology and behavior of this species during winter in spite of the popularity of their European counterpart. The present study was initiated in order to investigate the movements and feeding patterns of Black Oystercatchers during the period, December 1975 through April 1976. In a previous study (Hartwick 1976), the foraging of the birds was compared to a current model of optimal foraging theory (Royama 1970). This model suggests that predators should allocate their time according to the profitabilities of various prey items, spending most of their time concentrating on items which are more profitable. Another objective of the present study was to investigate this hypothesis for the case of oystercatchers feeding during the winter.

STUDY SITE

Most of the work centered on a large sand and mudflat in Lemmens Inlet near Tofino (lat. 49°N, long. 126°W) on the west coast of Vancouver Island (Fig. 1). Lemmens Inlet is a portion of Clayoquot Sound lying approximately 3 miles from the outer exposed coast and 11 miles from the main breeding site in the area (Cleland Island). During the winter these mudflats serve as feeding and roosting sites for many species and large flocks of oystercatchers were observed to use the flats at that time. The invertebrate fauna of the inlet is a mixture of organisms characteristic of both exposed and semiprotected environments. The dominant organism, at least in terms of numbers, is *Mytilus edulis*, the common bay mussel, which forms extensive beds over much of the area of the mudflats.

METHODS AND MATERIALS

Observation posts were established at four locations in the mudflats, always on the shore of an island. Whenever possible, observations were made over entire tidal cycles (for example, from a high tide through to the next high tide). On each observation day the total number of oystercatchers using the mudflats was recorded. Movement patterns into and out of the mudflats and within the mudflats were also noted. The diet of the birds was recorded from observations made by telescope. It was usually possible to identify a food item directly or by the feeding behavior of the birds. The mussel beds occurred as relatively discrete units and the relative use of the various beds by the birds was estimated by recording the time spent feeding in each bed. Feeding rates were measured for various mussel beds by recording the number of successful attacks in a given time at various stages in the tide cycle. Mussels that had been fed on by the birds were collected for measurement. The obvious tracks of the birds in the mud aided in this process. The total time spent feeding and roosting was also noted.

The primary mussel beds used for feeding by the Black Oystercatcher were surveyed to determine their tidal height, area, and density. Transects were made through the mussel beds and mussels were collected within a 0.5-m square at random intervals along the transects. Mussels in the quadrants were counted and measured. Samples were also taken in mussel bed areas not normally used by the oystercatchers.

Additional counts and observations were made by boat trip to the outer reefs and to Cleland Island, the main breeding site for these birds in this area. These trips have also been made at various times in the year over a 5-year period.

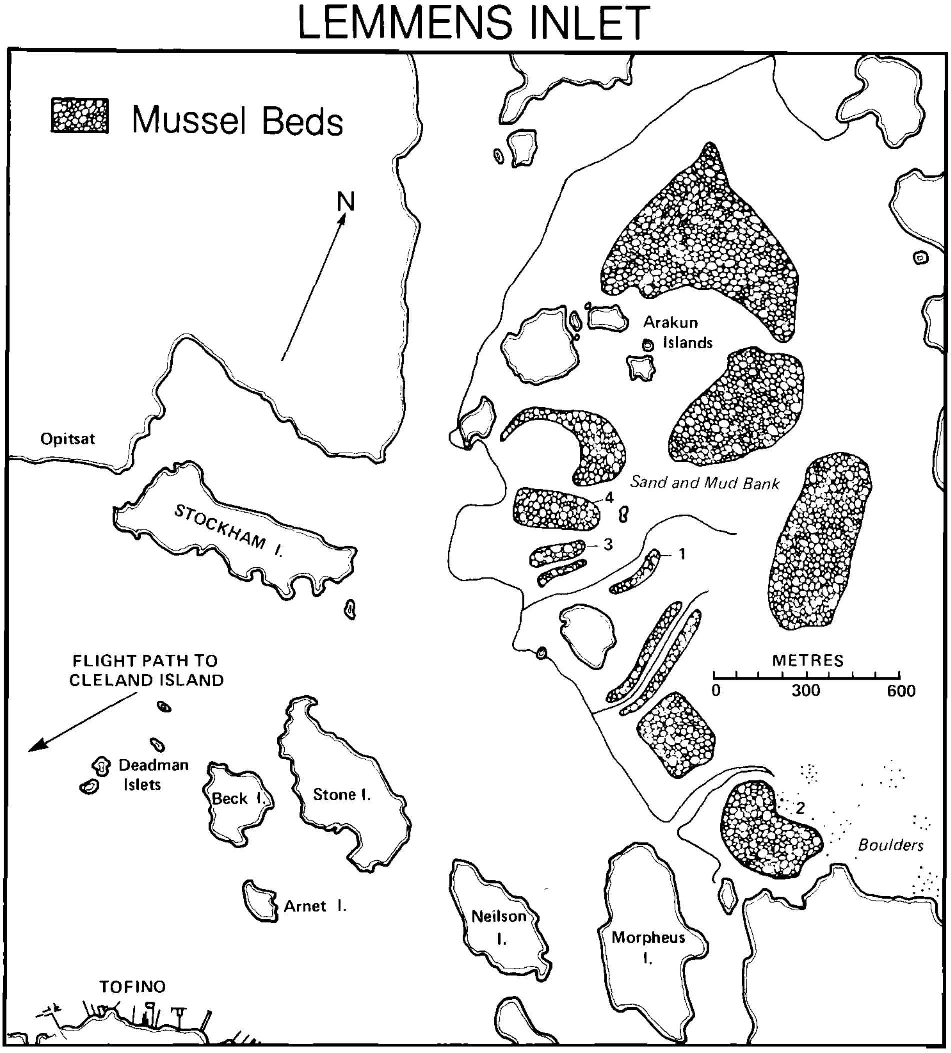

FIGURE 1. Study site at Lemmens Inlet in Clayoquot Sound, Vancouver Island.

OBSERVATIONS AND RESULTS

Distribution and Numbers of Birds

Visits to the area in the fall indicated little or no use of the mudflats at that time with most oystercatchers still out on exposed rocky shores, although sightings of flocks in protected areas have been reported as early as November (D. Hatler, pers. comm.). By December, there is consistent use of the mudflats for feeding and this continues through April after which time most birds again appear on exposed rocky shores. Boat trips to outer reefs indicated use of rocky shores by at least some of the birds throughout the winter, generally occurring as small flocks. Oystercatchers were observed on Cleland Island at various times throughout the winter and in March over 50 oystercatchers were spotted on the island with some showing obvious pairing and territoriality. In October (1976) only small

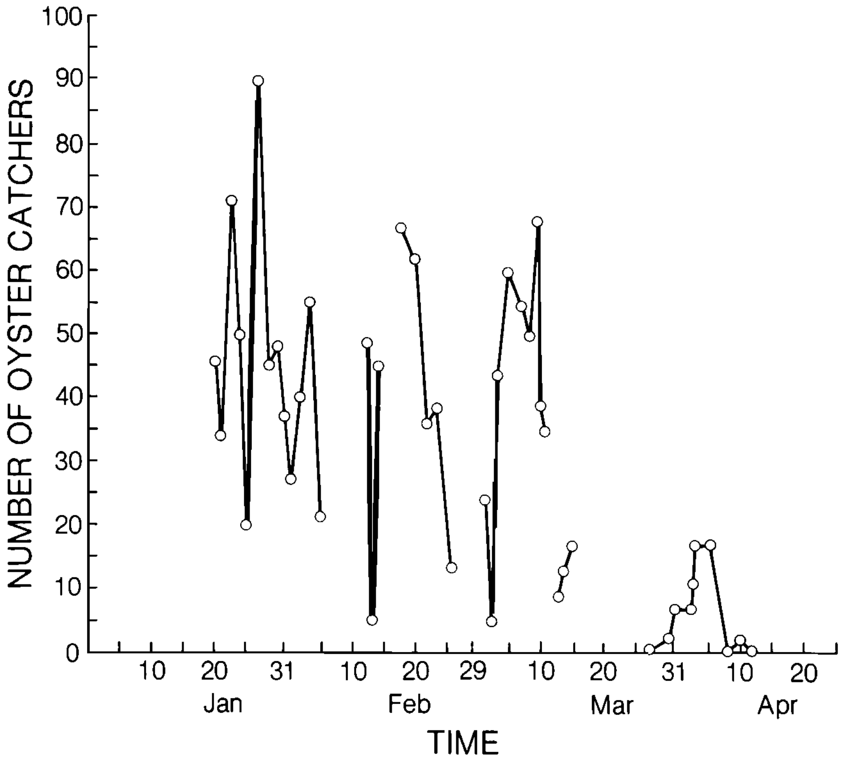

FIGURE 2. The number of oystercatchers observed on the mudflats of Lemmens Inlet.

numbers were observed in the breeding area and these generally left the island for the day, returning to roost at night.

The number of oystercatchers observed on the mudflats varied throughout the season from as many as 90 birds on 27 January to very few or none during observation periods in April. Use of the mudflats by these birds was generally heavy in the period from January to early March with numbers falling off in mid-March and remaining low thereafter (Fig. 2). Aside from this seasonal trend, fluctuations in numbers of birds appeared to be unrelated to tides, times, or general weather patterns although some low counts were associated with stormy weather (13 Feb.).

MOVEMENT PATTERNS OF OYSTERCATCHERS

Daily Movements to and from Feeding Area

The Black Oystercatchers did not roost in the mudflats overnight, but returned each evening to reefs and roosting sites out in more exposed areas (Fig. 1). Each morning Black Oystercatchers would fly into the feeding area in small groups from a westerly direction. The birds called repeatedly while flying, often being answered by distant birds already in the feeding area. Incoming flocks were frequently observed to land in the vicinity of birds that had been calling.

In the evening or late afternoon the oystercatchers left the feeding area of the mudflats for the open coast as a single large flock. The behavior of the birds getting ready to depart was very distinctive and repeated each day. One bird would begin calling, soon to be joined by all the others in the flock. Flight from the area as a single flock would soon follow once many birds had started calling.

The timing of arrival and departure from the feeding area was influenced by the tidal cycle. Arrival in the feeding area in the morning was usually coordinated with the low tide so that if the tide was high early in the day, the flock would not show up until the late morning or early afternoon. Similarly, once the mussel beds were covered by a rising tide the flock tended to leave the feeding area and fly to the open coast. The flock did not usually remain in the feeding area in late afternoon or evening unless the mussel beds were exposed and in all cases, the birds left the area before dark.

Movements within the Feeding Area

At high tide, Black Oystercatchers in the mudflats usually roosted on the tip of a small, bare rock in the middle of the mudflats. As the tide dropped to the level of *Fucus* growing on rocks in the mudflats, the oystercatchers would leave the roosting site in small numbers and begin foraging in the *Fucus* zone. As the tide drops lower the oystercatchers begin moving into and foraging in the mussel beds as they become exposed. The mussel beds used by the flock for feeding are exposed by a falling tide in this order: Area 4, Area 2, Area 3, Area 1, and the N-S channel beds. The oystercatchers move from bed to bed as they are exposed up to the point where the lower beds are exposed. From that point to low tide the movement into a particular feeding area within the mudflats is less predictable.

A period of roosting as a single flock usually occurs at or near the time of low tide. This is especially true if the birds have been feeding as the tide goes out. The earlier or later in the day the low tide occurs, the less likely the birds are to roost. Roosting invariably occurs at the water's edge and was rarely observed within a mussel bed.

Once low tide is reached and the tide begins to flood the mudflats the birds present usually feed continuously until the last mussel bed is covered. Once again, the movement into the various feeding areas follows the pattern with which they are covered by the tide. Time spent foraging in a feeding area is influenced by rate of flow of the tide, the presence or absence of other oystercatchers in the feeding area, and disturbances from outside sources. On a flooding tide, Black Oystercatchers are observed to forage in mussel beds along the line of the advancing water. Since Area 4 is the highest feeding area available, all the oystercatchers that are present in the mudflats will eventually be forced to forage there when the tide is at a certain level. Once Area 4 is covered the Black Oystercatchers fly to their roosting site in the mudflats. The length of time spent here depends on the time of day and, to some extent, on the weather.

SURVEY OF THE MUSSEL BEDS

The survey of the mussel beds used as primary feeding areas indicated that Area 4 was the largest and had the highest density of mussels. Area 2 was roughly the same size but contained considerably fewer mussels (Table 1). Area 3 was half the size of 2 and 4, but had a density of mussels halfway between that of Areas 2 and 4. The North Arakun mussel beds which were not used by the birds to any extent were extensive but had considerable amounts of eel grass associated

TABLE 1
MUSSEL BED CHARACTERISTICS

Location	Area (m²)	Tidal height (ft.)	Density (mussels/m²) (range in parentheses)	Time foraging[a] (%)
Area 1	3,606	4.1–5.8	524 (0–1208)	1.9
Area 2	32,000	4.9–6.3	548 (0–888)	18.8
Area 3	17,825	4.7–6.6	800 (244–1720)	28.6
Area 4	36,822	6.9–8.0	1182 (0–2332)	43.4

[a] Based on 55 hours of observations on 15 different days over a 3-month period.

with them. The size distribution of mussels in the North Arakun beds showed a mean size of 51.4 mm, compared to a mean size of 30.83 in Area 4. The density of mussels in the North Arakun beds was roughly 90 mussels/m², less than $^1/_{10}$ the density of Area 4. The mean time periods over which each bed was washed by waves were determined. This time of vulnerability varied with a mean of 31.2 min for Area 4, 57.2 min for Area 3, 47.5 min for Area 2, and 56.6 min for Area 1, based on 21 observations.

FORAGING RESULTS

Size and type of prey.—Black Oystercatchers on the mudflats of Lemmens Inlet fed exclusively on the mussel *Mytilus edulis.* Mussels fed on by the birds varied in size from 2.13 cm to 7.23 cm with a mean size of 5.0 cm based on a sample of 1428 mussels from Areas 1, 2, and 3. The size distributions of mussels taken from the various beds were similar in spite of significant differences in the size distributions of mussels in the beds. Figure 3 illustrates the size distribution of mussels taken by the birds for all samples combined. The selection of similar-sized items from beds of varying compostion resulted in a clear selection of relatively large mussels from beds in which the mean size of mussel was relatively small.

Use of the feeding areas.—Since the oystercatchers feed in mussel beds only when they are washed by water it is possible to estimate the amount of time the mussel beds are available to the oystercatcher and compare this with the amount of time the oystercatcher actually spends in the feeding area. Feeding in this area does not occur at night so this estimate is based only on tidal cycles during the

TABLE 2
FEEDING RATES (MUSSELS/MIN)

Tide condition	*Fucus* zone	Area 1	Area 2	Area 3	Area 4	N-S channel
Exposed	.1	.875	1.04	.514	.96	.99
Flooding	–	–	1.058	.428	.97	.85
Ebbing	.38	–	–	1.07	.98	–
No. of birds observed	5	1	9	5	19	8

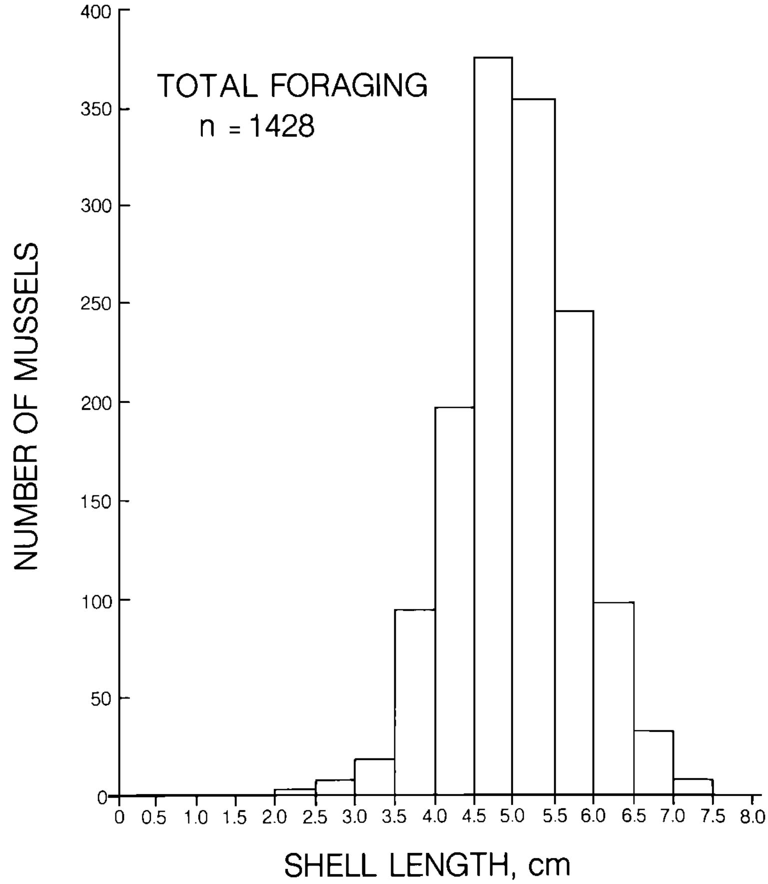

FIGURE 3. Size distribution of mussels taken by oystercatchers.

daylight hours. Of the total amount of time the mussel beds are available to the Black Oystercatcher, the birds spend roughly 53% of this time in the feeding area. A further breakdown of this figure showed that the birds were roosting approximately 52% of the time and feeding for 48% of the time. Thus the Black Oystercatcher uses only 25% of the time that the mussels are vulnerable for actual foraging.

This foraging time is distributed over the various beds. The percentage of time spent feeding in each area varied from a low of 1.9% in the *Fucus* zone to a high of 43.4% in Area 4 (Table 1).

Feeding rates.—The mean feeding rates of birds varied from a low of 0.1 mussels per minute in the *Fucus* zone while that zone was exposed, to a high of 1.06 mussels per minute in Area 2 during a flood tide (Table 2). The overall mean feeding rate for Areas 2, 3, and 4 was 0.9 mussels/min.

DISCUSSION

On the basis of this study and general observations, it would seem that Black Oystercatchers can be found on rocky exposed shores throughout the year but make use of protected mudflats to a varying extent especially in the winter. Since winter storms are common in the area it is surprising that the birds still utilize the exposed areas. The general impression, however, is that they are strongly tied to the breeding area and to nearby reefs. At this point it is difficult to judge the relative importance of protected mudflats. There is considerable variation in the numbers of oystercatchers using the mudflats at Lemmens Inlet. Storms do not appear to drive the birds into the bays and even in rather heavy seas they can be observed in flocks on the lee side of the islands and reefs. Total counts in the area suggest that most birds remain in Clayoquot Sound throughout the year and when they are not in protected inlets like Lemmens Inlet they are on reefs and rocky shores closer to the main breeding area. Several times, birds banded on Cleland Island were observed in the flocks using the mudflats supporting the idea that birds seen on the mudflats breed nearby.

There was no indication that the birds were feeding at night and they followed a consistent pattern of leaving the mudflat in the evening. Whether they fed on exposed shores at night was not determined but it seems rather doubtful under winter conditions.

Some interesting differences exist when the Black Oystercatcher is compared to its European cousin. For example, Black Oystercatchers ignored cockles (*Clinocardium nuttalii*) and other potential food items on the mudflats and concentrated on mussels, *M. edulis,* using the same stabbing method as they do with *M. californianus* on exposed shores. The restricted diet differs considerably from the diet of these birds during the breeding season when they can be observed feeding on a wide variety of items. Such a restriction suggests that food is not in short supply and, indeed, that seems to be the case at least at this time. On the other hand, large numbers of other species of birds including crows, starlings, gulls, and waterfowl use the same mudflat and it may be that diet restriction is somehow related to their presence. However, only gulls have been observed to directly interfere with the foraging of the oystercatchers.

The beds most used by the oystercatchers were those occurring in the open away from the shores of islands, closest to the open water, in the direction of the breeding area, and containing the greatest densities of mussels. The rather limited use of the mudflat area as a whole suggested that the birds would have minimal impact on the mussel beds at this time. Calculations based on their use of particular beds and their observed feeding rates support this impression. For example, an oystercatcher feeds in Area 4 an average of 50 min/day with a mean feeding rate of 0.97 mussel/min, therefore consuming approximately 50 mussels/day from this bed. If the maximum number of 90 birds were present then they would remove 4500 mussels/day from the bed. This is a maximum estimate probably much larger than the actual rate of predation. The estimated number of mussels in Area 4 was 43,523,600 and, since the birds utilized the beds primarily in the winter months, the birds probably had a minimal effect on the mussel populations at their present abundance.

The oystercatchers may even be aiding the survival of the mussel beds by their foraging. The empty shells of the eaten mussels remain within the matrix of the clump and are then available for mussel spat to settle on. In a shifting, loose substrate such as a mudflat, surfaces for settlement are at a premium, and we have observed on many occasions numbers of juvenile mussels growing on or within an empty shell. Thus the removal of the mussel, but not its shell, by the oystercatcher is effectively creating more space for larval settlement.

The relative use of the different mussel beds is of great interest. The percentage of time spent feeding in any bed increases with the density of mussels in the bed. Differences in the sizes of the areas and the lengths of time during which they are washed by waves do not explain the relative use of the beds. Presumably, the birds are responding to profitability differences (Royama 1970) in the beds. Thus, a higher density of mussels would result in a greater biomass return for a given hunting period. On the other hand, the feeding rate estimates do not necessarily support this idea, although the sample size is admittedly relatively small.

The restricted diet is also interesting. Mussels are probably the most profitable of food items available on the mudflats. They are both numerous and accessible. Nevertheless, Royama's model is based on the idea that predators will continually sample other prey in order to compare profitabilities over time and space. The Black Oystercatchers in Lemmens Inlet appear to feed only on mussels without sampling other items. Perhaps relative profitabilities do not change on the mudflat over the winter in which case the observed behavior would represent a most efficient pattern.

Further studies are required to determine how much feeding occurs on rocky exposed shores during winter. The amount of use of the mudflats may depend on feeding conditions in other areas. At present there is no satisfactory explanation for the pattern of variation in numbers using the mudflats and conclusions about the winter diet of the birds may be premature.

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FEEDING ECOLOGY OF THREE SPECIES OF PLOVERS WINTERING ON THE BAY OF PANAMA, CENTRAL AMERICA

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ABSTRACT.—The feeding ecologies of three species of plovers, *Charadrius semipalmatus, C. collaris,* and *C. wilsonia,* were studied on two beaches on the Pacific side of the Panama Canal Zone, Central America. The three species fed in mixed flocks on intertidal flats during low tide. Whereas *semipalmatus* and *wilsonia* foraged only at low tide, *collaris* foraged independently of the tidal cycle. The diets of each species were determined to be different by analysis of stomach contents. The prey of *wilsonia* had a mean size of 7.8 mm and consisted of 96% crustaceans, that of *semipalmatus* had a mean size of 1.8 mm and consisted of 82% polychaete worms, while that of *collaris* had a mean size of 3.7 mm and consisted of 50% insects and 27% crustaceans. The relationships among prey size, bill size, and body weight (complex in these species) are discussed. Values of dietary overlap between pairs of species ranged from 2 to 30%. *Semipalmatus* and *wilsonia* were found to be considerably more specialized in diet than *collaris*. These findings, along with published reports of the food habits of these species in other areas, indicate that the dietary differences observed are probably not the result of local competitive interactions. The low diversity of shorebirds, especially sandpipers, on the study areas seems best explained by physical properties of the substrate which make it unsuitable for birds which feed by probing. Scarcity of roosting sites rather than availability of food probably limits the populations size of plovers in the study area.

Samples of shorebirds collected over a short period of time at a given location typically show a high degree of food specificity, indicating specialization in food preferences (Reeder 1951, Ehlert 1964, Recher 1966, Brooks 1967, Bengston and Svensson 1968, Anderson 1970, Davidson 1971, Thomas and Dartnall 1971, Prater 1972). These preferences are often cited as proof of competitive interactions among the species studied. This impression is reinforced by the diversity of bill morphologies found in shorebirds (Lack 1971), by reports that species that forage together during migration and winter often use different feeding techniques (Recher 1966, Goss-Custard 1970, Burton 1972), and by observations that closely related species wintering in the same area tend to feed in different habitats (Ashmole 1970, Thomas and Dartnall 1971). On the other hand, Holmes and Pitelka (1968) report that sandpipers (Scolopacidae) with diverse bill morphologies eat almost identical food on their breeding grounds, and Recher (1966) and Thomas and Dartnall (1971) found that shorebird species with different bill morphologies often eat the same food during migration.

Most species of shorebirds move from inland breeding habitats to marine habitats during migration and winter. Along with this change in habitat there must be a change in the types of prey available. Since marine habitats contain a wider diversity of prey taxa than freshwater habitats, shorebirds in marine habitats might have wider prey diversity than they have in freshwater habitats. A change in prey taxa, however, does not necessarily mean that shorebirds are not food specialists, since they may be specialized to take prey of a limited morphological type, may specialize in the type of habitat in which they feed, or sometimes may be forced by competitive interactions to take a particular prey. Unfortunately, little is known about the diets of most species throughout the year in the different habitats in which they forage.

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Most studies of shorebird ecology have been based on sandpipers (Scolopacidae). Most sandpipers breed in northern latitudes and migrate south for the winter. Plovers (Charadriidae), on the other hand, are more cosmopolitan; many species are resident in temperate and tropical regions. Thus, although sandpipers may winter with species which breed in other areas, all species in a given location are away from their breeding grounds. In contrast, northern plovers often winter in areas where congeneric species are resident. Whether there are fundamental differences in the interactions among shorebird species in these cases is unknown; indeed, the effect of northern migrants on resident species at more southerly localities is poorly understood (Willis 1966). But there is reason to expect that birds spending all of their lives in one habitat are likely to show different feeding adaptations from birds which face radically different competitive interactions and conditions of food availability each season.

Three species of plovers winter in the Canal Zone: Semipalmated Plover (*Charadrius semipalmatus*), Collared Plover (*C. collaris*), and Wilson's Plover (*C. wilsonia*). The three species feed together in the same habitat, use superficially similar feeding techniques, but differ in size and bill morphology. Two of the species (*collaris* and *wilsonia*) winter within their known breeding ranges, while *semipalmatus* migrates in winter far to the south of its breeding range. We examined the roles of food supply, behavior, and morphology in the feeding ecology of these species.

MATERIALS AND METHODS

Charadrius semipalmatus breeds on the Arctic coast of North America south to northern British Columbia, James Bay, and maritime Canada, and winters from central California, the Gulf Coast, and South Carolina south to Chile and Argentina (A.O.U. 1957). *C. collaris* is found in tropical America from Mexico (Michoacan, Oaxaca, and Veracruz) south to Chile, northern Argentina, and Uruguay (Peters 1934, Warner and Mengel 1951, Eisenmann 1955, Storer 1960). Breeding records north of South America have been confirmed only for Mexico (Amadon and Eckelberry 1955, Storer pers. comm.) and Honduras (Monroe 1968). *C. wilsonia* breeds coastally from Virginia and Baja California south to the Caribbean coast of South America and Perú (A.O.U. 1957). Breeding records in Panamá and the Canal Zone include Aguaduce and Fort Amador (Ridgely 1976).

We studied and collected plovers on two beaches on the Pacific side of the Isthmus of Panama: Venado Beach (8°54′N, 79°36′W) at the mouth of the Río Venado, just south of Howard Air Force Base, Canal Zone, and Skeet Beach, 7 km to the northeast behind the skeet range at Fort Amador. Our study was carried out mainly between August 1972 and May 1973, with three or four visits to one or the other of the study beaches each week.

In this region tidal differences have a maximum range of about 6 m; typically 1000 to 1500 m of intertidal flats are exposed during low tide at Venado Beach and about 500 m at Skeet Beach. Both beaches differ from nearby Naos Beach (Dexter 1972) in having considerably greater areas exposed during low tides and in that most of the exposed areas are shallow mud rather than pure sand. The study area at Venado Beach is about 800 m along the beach by about 1200 m wide, while that at Skeet Beach is about 200 m along the beach by 500 m wide. The Venado Beach area is bounded on the east by a rocky headland interspersed with several small sand beaches and on the west by a sand spit beyond which is an area covered by water at low tide. The Skeet Beach area is bounded on the north by a low, rocky headland and on the south by the Amador Causeway. As determined by aerial photographs and ground observations, the surface of the study area at Venado Beach during low tide consists of about 74% mud (containing much fine sand), 21% sand (about 50% quartz sand and 50% ground shell), and 5% exposed rocks. The area at Skeet Beach is about 90% mud, 9% sand, and 1% rocks. About 15% of the area of the flats at both beaches is covered by small, shallow pools at low tide.

A detailed study of the intertidal fauna was not made. Spot-sampling of the fauna at both beaches indicated that its composition was essentially the same as, but more dense than, that found by Dexter

(1972) at Naos Beach (which lies within 8 km of both study areas). Dexter's value of 1443 invertebrates/m^2 is a likely minimum value for the beaches we studied.

Feeding birds were observed with 7× binoculars or a 20× spotting scope. The type of substrate used, feeding movements, and interactions among individuals and species were recorded.

From October 1972 to March 1973, 58 plovers (13 *semipalmatus,* 16 *collaris,* and 29 *wilsonia*) were collected for analysis of stomach contents. All the birds were saved as specimens, which have been deposited in the collections of the Museum of Zoology, The University of Michigan. The majority of the birds (38) were collected during October and November 1972 after migration had stopped. Forty birds were collected while feeding during low tide at Venado Beach, while the remainder were collected during high tide at Skeet Beach.

Stomachs were removed and placed in 10% buffered formalin within an hour of collection. They typically contained hard and soft parts of prey animals as well as some sand and gravel. In all cases in which soft material could be identified, it proved to be part of an animal for which hard parts were also present in the stomach. If the birds had also been eating soft prey which digested rapidly, leaving no trace, however, analysis based on hard remains in the stomachs would give a biased estimate of diet. Since we were unable to determine that any such soft animals were taken by the species studied, we feel justified in using only hard parts in our analyses of stomach contents. In any case, most of the birds were collected while feeding, and crushed but undigested animals were often found in the stomachs.

Identification and size estimates of the prey were made by comparing hard parts found in the stomachs with a reference collection of whole animals collected in the study areas. Crustaceans were identified by LGA, the remainder of the prey by JGS. Dr. Henry Stockwell aided in identifying Coleoptera. Size measurements were based on the greatest exposed part of the prey animal, e.g., carapace width for crabs and total body length for Coleoptera. As only the head of polychaete worms was exposed to the feeding birds, head width was chosen as the measure of the actual target presented to a feeding plover. Though this choice of measurement was arbitrary, it was both expedient and reasonable, since plovers did appear to obtain only the anterior portion of a worm.

RESULTS

In both 1971–72 (when no feeding studies were made) and 1972–73, *collaris* began arriving on the beaches in groups of up to six birds early in September. The place of origin of these birds is unknown; evidence that the species breeds in Panama is circumstantial (Eisenmann in litt., Ridgely 1976). By the end of September the wintering populations had stabilized, with 10 to 25 birds regularly found feeding on the flats. *Semipalmatus* first arrived in late August in small numbers, and migrating flocks continued to pass through the area until November. The birds found after mid-November appeared to be wintering locally. Up to 100 birds could be found on the flats at this time. *Wilsonia* suddenly appeared in numbers in late September, and by mid-October flocks of up to 200 wintering birds were found.

In the spring *collaris* left the study area starting about mid-February, and by the end of the month no individuals remained. By the end of February migrating *semipalmatus* flocks began to appear. From then until the middle of April the numbers of *semipalmatus* fluctuated greatly as migrants passed through Panama. Exactly when the local wintering birds left is unknown. Migration of *semipalmatus* continued at least into early May. Individuals of this species sometimes summer in Panama (Eisenmann 1951). Most *wilsonia* left the area in the last half of March. During the first week of April a few individuals of *wilsonia* were found among the flocks of *semipalmatus*. In 1972 no plovers were seen in the study areas between mid-April and mid-August.

In January 1973 mixed flocks of plovers roosting on Skeet Beach at high tide averaged 193 birds (range 41–350), of which about 68% (66–73%) were *wilsonia,* 28% (17–35%) were *semipalmatus,* and 3% (0–10%) were *collaris.*

TABLE 1

MEASUREMENTS OF *Charadrius* PLOVERS FROM THE CANAL ZONE

Species	N[a]	Mean bill length (mm)	Mean wing length (mm)	Mean body weight (g)
C. semipalmatus	7	12.2	118.4	39.4
C. collaris	14	14.6	93.5	28.3
C. wilsonia	36	20.6	115.1	55.1

[a] All specimens were collected in study area during 1971–73, but not all were used for stomach analyses. A few birds whose bills were damaged during collection are not included.

During low tide *semipalmatus* and *wilsonia* fed together in mixed flocks over the entire exposed area. *Collaris* was occasionally a member of these mixed flocks, but was usually found feeding on sandy areas nearer the high-tide line. The plovers fed in small groups of about 6 to 20 birds, spaced one to two meters apart. As the tide rose, these groups came together and occasionally moved on to dry beach to roost before being forced off the flats by the rising water. No obvious aggressive interactions were seen between the species or among conspecific individuals, although when one bird moved, the birds toward which it moved usually moved away from it.

During high tide *semipalmatus* and *wilsonia* roosted together on Skeet Beach. At that time they did not actively hunt for food, but did occasionally snap up prey which they encountered by chance. At high tide *collaris* sometimes roosted with the other two species but usually actively foraged on the beach and on nearby gravelly or short-grass areas. *Semipalmatus* and *wilsonia* foraged only at low tide, while *collaris* foraged independently of the tidal cycle.

The feeding behavior of the three species is typical of most plovers (Pearson and Parker 1973, Burton 1974): the birds run several steps, stop and stare, and then peck at prey. This sequence is performed repeatedly by a small group of birds moving along in parallel paths. The species studied here are strictly visual feeders. The actual method of prey capture is distinctive for each species. *Semipalmatus* catches prey by tipping forward at the ankle so that the tail is raised as the head goes down. *Collaris* usually jabs downward with little or no tipping of the entire body, although the ankle is also bent. This difference in feeding motion is correlated with the differences in body size and bill length of the two species; *semipalmatus* is a taller bird with a shorter bill compared to *collaris* (Table 1) and thus while feeding must bend over more in order for its bill to touch the ground. *Wilsonia* captures prey by lunging at it for up to one meter. Whereas the other two species usually take a few steps during prey capture, *wilsonia* actually runs during its forward lunge. At the moment of capture the bird is usually in a low crouch with neck extended.

Size measurements from birds collected in the study area are given in Table 1. No significant differences were found between the sexes. The size relationships among the species are complex. In body weight *wilsonia* is the largest bird and *collaris* the smallest. *Semipalmatus* has the longest wings, probably a reflection of its more migratory habits (Salomonsen 1955). *Wilsonia* has the largest bill, *semipalmatus* the shortest, while *collaris,* with lowest weight and wing length, has a bill intermediate in size. The ratio of bill lengths (in the order

TABLE 2

Diets of Three Species of *Charadrius* Plovers Wintering on the Bay of Panama, Central America, as Determined by Stomach Contents Analysis

	C. semipalmatus			*C. collaris*			*C. wilsonia*		
	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)
Prey	N = 408	13		185	15		188	26	
Brachiopoda									
Inarticulata									
Atremata (*Lingula*?)	4.90	15.4	5.4–7.3	–	–	–	–	–	–
Mollusca									
Gastropoda									
Archaeogastropoda									
Neritidae	0.49	7.7	2.3	–	–	–	–	–	–
Mesogastropoda									
Naticidae	1.72	15.4	1–2	1.08	6.67	2	–	–	–
Neogastropoda									
Nassariidae	0.49	15.4	1–2	0.54	6.67	1–2	–	–	–
Marginellidae	0.49	15.4	2	–	–	–	–	–	–
Entomotaeniata									
Pyramidellidae	4.90	23.1	2–4	–	–	–	–	–	–
Annelida									
Polychaeta									
Nereidae	72.79	76.9	0.5–2.5	12.97	26.7	1–2	1.07	7.7	2
Glyceridae	6.86	38.5	1–2	0.54	6.7	1–2	–	–	–
Sp. 1	1.72	23.1	1–2	0.54	6.7	1–2	–	–	–
Sp. 2	0.98	7.7	1–2	–	–	–	–	–	–
Arthropoda									
Crustacea									
Isopoda									
Ancinus sp.	0.49	7.7	4	12.97	26.7	3–4	4.28	7.7	3–4
Sp. 1	–	–	–	1.62	13.3	4–6	–	–	–
Amphipoda									
Gammaridae	–	–	–	–	–	–	1.07	3.8	2
Decapoda									
Penaeidae (*Penaeus brevirostris*)	0.24	7.7	5	2.16	13.3	4–6	2.14	7.7	4–6
Caridae (*Palaemon*)	–	–	–	3.24	33.3	3–5	–	–	–
Paguridae (*Paguristes*)	–	–	–	–	–	–	0.54	3.8	1
Hippidae	–	–	–	0.54	6.7	6	–	–	–
Brachyrhyncha									
Uca panamensis	–	–	–	0.54	6.7	6	21.39	46.2	6–15
Uca inaequalis	–	–	–	4.86	13.3	3–9	11.22	23.1	3–9
Uca beebei?	–	–	–	–	–	–	0.54	3.8	10
Eurypanopeus transversus	0.24	7.7	1	–	–	–	19.79	38.5	6–10
Speocarcinus ostrearicola	–	–	–	–	–	–	10.70	11.5	7–11
Callinectes arcatus (juv.)	–	–	–	0.54	6.7	3	5.35	23.1	4–10
Goneplacid ? crab	–	–	–	–	–	–	4.81	7.7	7–11
Xanthid crab	0.24	7.7	4	0.54	6.7	10	10.16	30.8	7–11
Panopeus chilensis	–	–	–	–	–	–	2.67	7.7	6–9
Eriphia squamata	–	–	–	–	–	–	0.54	3.8	9
Crab megalopa	0.24	7.7	1	–	–	–	0.54	3.8	1
Insecta									
Orthoptera (non-roach)	0.49	15.4	6.5–10.3	10.27	53.3	2.5–14	–	–	–
Blattodea	–	–	–	1.08	13.3	5	–	–	–
Coleoptera									
Carabidae 1	0.24	7.7	5.5	–	–	–	–	–	–
Carabidae 2	–	–	–	0.54	6.7	3	–	–	–
Carabidae 3	–	–	–	0.54	6.7	5	–	–	–
Histeridae	–	–	–	0.54	6.7	2	–	–	–
Staphylinidae	–	–	–	0.54	6.7	3	–	–	–
Cucujidae	–	–	–	0.54	6.7	2.5	–	–	–
Tenebrionidae 1	–	–	–	0.54	6.7	3	0.54	3.8	0.5
Tenebrionidae 2	–	–	–	1.08	6.7	3.5	–	–	–
Tenebrionidae 3	–	–	–	0.54	6.7	3.5	–	–	–
Tenebrionidae 4	–	–	–	0.54	6.7	4	–	–	–

TABLE 2. (CONTINUED)

	C. semipalmatus			*C. collaris*			*C. wilsonia*		
	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)	% prey individuals	Frequency (% stomachs)	Size range (mm)
Prey	N = 408	13		185	15		188	26	
Scarabaeidae 1	–	–	–	0.54	6.7	2.5	–	–	–
Scarabaeidae 2	–	–	–	0.54	6.7	2.5	–	–	–
Curculionidae 1	–	–	–	5.40	26.7	3.5	–	–	–
Curculionidae 2	–	–	–	1.08	6.7	4	–	–	–
Curculionidae 3	–	–	–	0.54	6.7	6.5	–	–	–
Curculionidae 4	–	–	–	1.08	6.7	4	–	–	–
Coleoptera 1	–	–	–	1.08	6.7	2.5	–	–	–
Coleoptera 2	–	–	–	1.08	6.7	3.5	–	–	–
Coleoptera 3	–	–	–	0.54	6.7	4	–	–	–
Coleoptera larvae	–	–	–	1.62	6.7	4	–	–	–
Hymenoptera									
Formicidae	1.22	30.8	2.5	16.76	73.3	1.4–6	2.67	11.5	3.5–5.5
Other Hymenoptera	0.73	15.4	4.5	2.16	20.0	5	0.54	3.8	5
Insect sp. ?	–	–	–	0.54	6.7	3	–	–	–
Animal sp. ?	–	–	–	0.54	6.7	?	–	–	–
Seed 1	–	–	–	0.54	6.7	1	–	–	–
Seed 2	0.49	7.7	3	2.70	6.7	3	–	–	–
Seed 3	–	–	–	2.70	6.7	1	–	–	–

collaris:*semipalmatus*:*wilsonia*) is 1.20:1.00:1.69; the ratio *collaris*:*wilsonia* is 1.00:1.41.

Except for four birds (one *collaris* and three *wilsonia*, all collected at Venado Beach), all the stomachs examined contained food items. Table 2 gives the results of the stomach contents analyses. Since we found no dietary differences between the sexes or between samples taken in different months or from different beaches, all samples of a species were lumped for final analyses. The diet of each species is distinct: *semipalmatus* takes about 82% polychaete worms, *collaris* takes 50% insects and 27% crustaceans, while *wilsonia* takes 96% crustaceans.

Figure 1 shows the percent of individuals of each general type of prey in all samples for each species, as well as the frequency of occurrence (percent of stomachs) for each type of prey.

Figure 2 is a plot on probability paper of prey size vs. cumulative percent of items in the diet. A straight line on such a plot would indicate a statistically normal distribution in the sizes of the prey taken. Clearly the diet of *semipalmatus* is skewed toward smaller food items (mean size 1.81 mm) while that of *wilsonia* is skewed toward larger items (mean size 7.82 mm). The size distribution of the prey of *collaris* shows a preference for prey near the mean size of 3.70 mm. The result for *semipalmatus* may be due to the method by which we measured the size of its major prey, polychaete worms.

Table 3 gives the percent overlap for the diet of each species pair calculated by the method of Horn (1966) for determining alpha and by the sum of shared frequencies, as used by Baker and Baker (1973) and Holmes and Pitelka (1968) for comparing shorebird diets. The same calculations were made for overlap

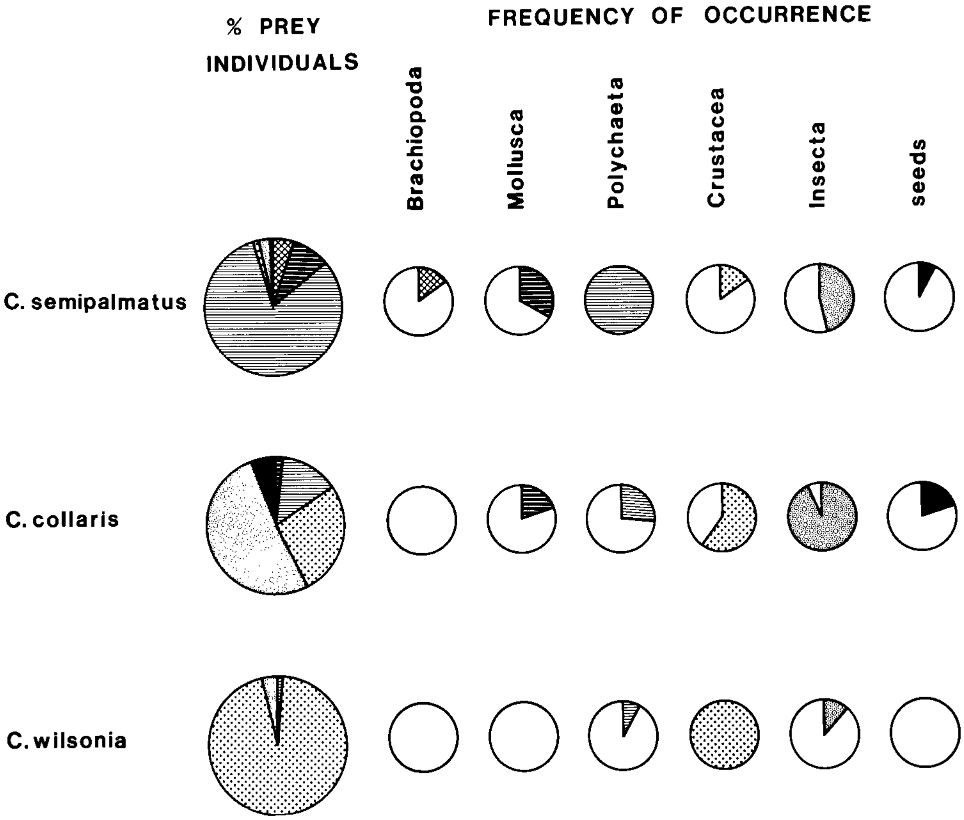

FIGURE 1. Percentage composition of stomach samples from three species of *Charadrius* plovers from the Canal Zone. Each complete circle represents 100%. Frequency of occurrence is the percentage of stomach containing the indicated prey.

based on taxon of prey items and on size of prey items. The resulting overlap measurements are similar whether based on taxon or size of prey.

The degree of specialization in feeding habits of the plovers may be examined by comparing the diversities of their diets. Table 4 gives the results of calculation of the informational-theoretical measure of diversity, H, based on natural logarithms (Lloyd et al. 1968) of the diets of the three species. The calculations were made, first, by using each prey species as a separate category of prey and, second, by lumping the prey into larger taxonomic units. The second calculation assumes

TABLE 3
DIETARY OVERLAP FOR SPECIES PAIRS OF PLOVERS FROM THE CANAL ZONE

	Percent overlap based on taxon of prey		Percent overlap based on size of prey	
Species pair	Alpha × 100	Sum of shared frequencies	Alpha × 100	Sum of shared frequencies
C. semipalmatus-C. collaris	30.7	18.7	21.1	29.9
C. collaris-C. wilsonia	19.7	17.1	6.2	15.1
C. wilsonia-C. semipalmatus	2.8	4.5	1.9	5.2

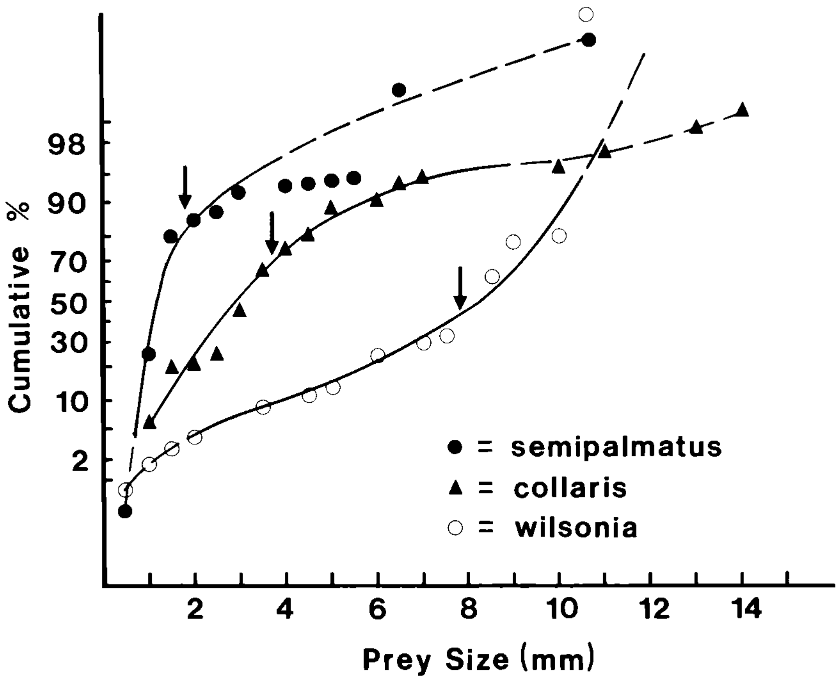

FIGURE 2. Distribution of prey size for three species of *Charadrius* plovers in the Canal Zone. The arrows indicate the mean prey size for each species.

that the plovers do not make use of fine taxonomic distinctions in what they eat, distinguishing crabs from worms but making no distinctions among different kinds of crabs or different kinds of worms.

We have evidence, however, that the plovers do distinguish between two different kinds of crabs. Some species of crab found on the flats use a cryptic posture or coloration as a defense mechanism, while others assume a lateral spread defense posture along with attack autotomy of the chelipeds if pursued (Robinson et al. 1970). Only crabs using cryptic postures or coloration were found in the plovers' stomachs. Only females of *Speocarcinus ostrearicola,* a species in which only the male uses the lateral spread posture, have been identified in the plovers' stomachs.

The diversity measures using each prey species as a separate category indicate that *semipalmatus* is more specialized (shows lower diversity) in its diet than the

TABLE 4
INDICES OF DIVERSITY OF DIET FOR THREE SPECIES OF *CHARADRIUS* PLOVERS

Species	Single prey taxa		Lumped prey taxa	
	H	e^H[a]	H	e^H[a]
C. semipalmatus	1.145	3.1	0.801	2.1
C. collaris	2.636	14.0	1.942	7.0
C. wilsonia	2.184	8.9	0.517	1.7

[a] e^H = number of equally common species in the diet.

other two species. When prey are lumped, however (the categories used were brachiopods, gastropods, polychaete worms, isopods, amphipods, shrimp, crabs, orthopterans, beetles, hymenopterans, and seeds), the diversity measures decrease unequally for the three species. The greatest drop in diversity occurs in *wilsonia*. The lumped diversities indicate that both *semipalmatus* and *wilsonia* are considerably more specialized in diet than is *collaris*.

DISCUSSION

Our results show a clear separation in the diets of the plovers studied. The mean prey sizes (1.8 mm for *semipalmatus*, 3.7 mm for *collaris*, and 7.8 mm for *wilsonia*) correlate well with the average bill lengths (12.2, 14.6, and 20.6 mm, respectively) of these species but not with their body weights (see Table 1). Holmes and Pitelka (1968) found a partial separation of modal size of prey to be correlated with bill size in sandpipers. Ashmole (1968), however, has shown that bill length alone is a poor indicator of prey size in some groups of sympatric terns. Hespenheide (1971) found body weight to be a better predictor of mean prey size than bill size for insectivorous birds. The discrepancy between our results and Hespenheide's is probably related to our choice of measurement used to estimate the size of the prey of *semipalmatus*. Had we used prey body weight as a measure of size instead of length (or width of head in the case of polychaetes), our results would probably agree with those of Hespenheide.

There is, however, a clear separation in the kinds of prey taken, regardless of size. *Semipalmatus* eats principally polychaete worms, *wilsonia* eats mainly crustaceans, while *collaris* eats a wide variety of prey.

The only other reported values of food diversity for shorebirds are those of Recher (1966). Since he did not report the details of his calculations, one must use caution when comparing his indices with ours. Of the species he studied, *semipalmatus* was the most specialized in diet. The dietary diversity that we find for *collaris* is almost twice that of the species with the most diverse diet in Recher's study.

Whether calculated according to taxon or prey size, overlap is about 25% in the diets of *semipalmatus* and *collaris*, about 10–20% in the diets of *collaris* and *wilsonia*, and about 4% in the diets of *wilsonia* and *semipalmatus* (Table 3). Holmes and Pitelka (1968) found about 15–88% food overlap for sandpipers on their Alaskan breeding grounds during a season when food was abundant. Except from late June to early July, when the variety of available prey was greatest, overlap in diet was greater than 30%. From the data of Recher (1966) and Anderson (1970) we calculated an average value of 52% (30–88%) overlap in diet for six congeneric pairs of shorebird species using about the same habitat for feeding during migration. Compared to other reports for shorebirds using the same or similar habitats, the overlap in food which we find is low. This is probably a reflection of an abundant and diverse food supply.

The similarity in overlap measurements, whether based on taxon or size of prey, may be fortuitous, considering how the size of the prey of *semipalmatus* was measured, or may be due to the relationship between size and taxon of prey (Hespenheide 1971). The specialization of prey type in *semipalmatus* and *wilsonia* indicates that attributes other than size are important in identifying potential prey.

The differences in morphology and diet which we found among these species might be the result of local competitive interactions, or they might reflect selective forces operating during other times of the year or in different locations. Most important would be independent specialization on different food organisms. Overlap or its absence, considered alone, do not necessarily indicate competition or its absence (Vandermeer 1972, contra Levins 1968, Baker and Baker 1973).

Semipalmatus is found mainly on marine coasts during the winter; it breeds throughout a large inland area as well as in coastal habitats (Bent 1929, Todd 1963, Godfrey 1966, JGS pers. obs.). During migration it is found throughout North America wherever conditions are suitable for shorebirds (Bent 1929, Robbins et al. 1966, Parmelee et al. 1969). On inland areas the species takes mostly insects (Lönnberg 1903, Bent 1929), especially larvae (JGS pers. obs.). Cottam and Hanson (1938) found the stomachs of a nesting pair of *semipalmatus* collected in Labrador to be gorged with insects, spiders, and a few seeds. In coastal California (Recher 1966) and South Carolina (JGS pers. obs.) *semipalmatus* eats mainly polychaete worms, as it does in Panama. In addition, it has been observed to eat unidentified marine worms in Peru (Ashmole 1970), New Jersey (Stone 1937), and Massachusetts (JGS pers. obs.). Other reports (Forbush 1916, Reeder 1951) indicate that it exploits other marine food when it is abundant.

Instead of being a food specialist *semipalmatus* appears to adapt its diet to locally abundant prey. The only other shorebird which has been shown to be similarly opportunistic is the Dunlin (*Calidris alpina*) (Vielliard 1973).

That *semipalmatus* is more likely to eat brachiopods and mollusks and less likely to eat crustaceans than are the other two species may be related to its short bill. *Collaris* and *wilsonia,* with their longer bills, are better adapted to catch fast-moving prey (Ashmole 1968). Since on our study area *semipalmatus* and *wilsonia* use exactly the same habitat for foraging, it seems unlikely that they encounter potential prey species on the beaches with different frequencies. *Wilsonia,* however, is better equipped for capturing and subduing fast prey; since food is abundant, it can ignore other kinds of potential prey (which also tend to be smaller). *Semipalmatus,* on the other hand, may be limited to eating slower-moving animals or those which can be taken by surprise while partially emerged from their burrows. Recher (1966) found that larger species of shorebirds feed selectively on larger prey but also take some smaller prey, while smaller species eat all food items that they encounter. The diets of *wilsonia* and *collaris* show this pattern of feeding behavior.

Of the three species we studied, *wilsonia* appears to be most specialized in habitat and food. Throughout its range it is confined to marine beaches and mudflats (Bent 1929), where it feeds mainly on crustaceans, especially crabs (Bent 1929, Tomkins 1944, Palmer 1967). We have no evidence that its diet and feeding behavior in Panama differ from those found elsewhere.

Collaris is known from both coastal and inland habitats (Warner and Mengel 1951, Amadon and Eckelberry 1955, Haverschmidt 1968) and may breed in a variety of situations. Although Haverschmidt reported insects as the only known food, we found that marine organisms are taken in coastal situations. Why *collaris* does not exploit the intertidal area for all its food needs like the other two species is unclear. This question is particularly interesting because *semipalmatus,* which is also a generalist, seems to be able to specialize in our study area while *collaris* does not. *Collaris* is a tropical species. Tropical areas are characterized by high animal diversity but low abundance for any given taxon. Because of this perhaps there has been little selective pressure on *collaris* to specialize its diet. Conversely, *semipalmatus* occurs in subarctic and temperate regions where prey diversity is often low but where a given prey taxon may be superabundant. Selection has thus favored the ability to specialize in whatever prey happen to be locally abundant.

Since feeding habits of these plovers in Panama appear to be much the same as they are in areas where the three species do not occur together, we doubt that local competitive interactions are important in maintaining them. In our study areas the plovers have an abundant food supply. Dexter's (1972) estimate of 1443 invertebrates/m^2 for Naos Beach, Canal Zone, represents a lower limit for the abundance of prey animals on the beaches we studied. Recher (1966) found about 1300 animals/m^2 in the areas he studied in California. In addition, our observations of plovers leaving the flats to roost while up to 50% of the tidal areas were still available for feeding indicates that the birds were satiated before the incoming tide forced them off the flats. While this pattern held true for *semipalmatus* and *wilsonia, collaris* fed throughout the day independently of the tidal cycle. Bédard (1969) found a similar situation in his study of three species of auklets in Alaska during the breeding season. He reported that the species with the most diverse diet, *Cyclorrhynchus psittacula,* spent more time on the feeding grounds, which it shared with two species of *Aethia,* even though all of the species seemed to have access to the same feeding depths.

In spite of the large diversity and abundance of food in our study area, few shorebirds other than plovers used the area. Plovers are limited to surface prey. Recher (1966) argued that the diversity of the habitat and not the diversity of food organisms appears to limit shorebird species diversity. He found, however, that tidal flats had relatively high habitat diversity due to the stratification of food organisms within the substrate. A possible explanation for the apparent lack of other shorebird species in our area is the density of the substrate. Although we classified most of the intertidal area as mud, almost all the mud areas are thin layers of soft material over a harder sand substrate on which we walked without difficulty. The only shorebirds observed to feed by "probing" in our study areas were occasional Western Sandpipers (*Calidris mauri*); the maximum depth to which this species can probe is about 28 mm, however. A greater diversity of shorebirds was found on the mudflats near Panamá Viejo at the mouth of the Río Matias Hernández. There the substrate is soft mud, and deep-probing species such as dowitchers (*Limnodromus* sp.) were commonly observed. It seems reasonable that the low diversity of shorebirds on Venado Beach is related to a preference of many species for a softer substrate, which can be found no more than 20 km away.

The populations of plovers on our study areas may be limited not by availability of food, but rather by a scarcity of roosting sites. During high tide the exposed beach is narrow at both Venado and Skeet beaches. Both beaches are often heavily used by people. Plovers were never observed to roost on Venado Beach, and those that roosted on Skeet Beach were frequently disturbed, sometimes leaving the beach entirely. Neither beach was used as a roost at night. The nocturnal roosting sites of the birds we studied remain unknown, but probably are offshore rocks, where during the day we found dense aggregates of plovers, gulls, terns, and some herons. At Palo Alto, California, Recher (1966) found that available space appeared more important than food supply in limiting the size and density of migrant shorebird populations. Feare (1966) suggested that the numbers of wintering Purple Sandpipers (*Calidris maritima*) were limited by the availability of roosting sites on Robin Hood's Bay, North Yorkshire. These observations agree with the belief expressed by Miller (1967) that features of the habitat required for breeding or shelter may be more limiting than food for some species.

Since shorebirds are common, conspicuous birds which occur in relatively simple habitats, they are well suited for studies of feeding ecology and competition for food. Studies of sandpipers, however, are complicated by the large number of species which commonly occur together, making necessary consideration of many simultaneous species interactions, and by the ability of a species to use more than one feeding method, thus increasing the proportion of the habitat it can exploit. Studies of plovers, on the other hand, have fewer of these complications, since only a few species occur together at one time and since plovers are restricted to feeding on the surface of the substrate. Nevertheless, there is considerable opportunity for the comparative approach, since many different species mixes are available at different locations; *semipalmatus*, for instance, can be found with one or more of at least six different congeners at some time during the year.

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TERRITORIALITY IN NON-BREEDING SHOREBIRDS

J. P. Myers, P. G. Connors, and F. A. Pitelka[1]

Abstract.—During the non-breeding season, many shorebirds defend feeding territories. Our studies in coastal California and eastern Argentina examine the extent of shorebird 'winter' territoriality, and describe its ecological context. Eleven species in California and 13 in Argentina defend territories for varying periods of up to several months' duration. The expression of territoriality differs in extent between species, individuals, and habitats, being most strongly developed in local populations foraging on the short-grass pampas and seasonal wetlands of coastal Argentina. Explanation of this variation may best be sought in terms of individual responses to local habitat conditions affecting the energetic costs and benefits of defending foraging sites. One such habitat parameter appears to be the length of time that local areas are available for foraging. Other hypotheses, such as preparing individuals for breeding behavior or decreasing predation risk, are considered and tentatively rejected.

Many shorebirds defend territories in the winter. Yet their activities frequently pass unnoticed, overshadowed by the spectacular size and unison of nearby winter shorebird flocks. The striking contrast between these two spacing strategies, often juxtaposed across a defended boundary, poses a fundamental ecological and evolutionary question: Why should a bird indulge in territorial defense while others survive nonaggressively? In this paper we establish a framework for considering this question by examining the characteristics and extent of shorebird non-breeding territoriality.

Our data stem from several seasons' work in two localities, including 18 months observing North and South American species overwintering in coastal Buenos Aires Province, Argentina, and three winters at Bodega Bay in central coastal California. During these studies we have concentrated on the White-rumped (*Calidris fuscicollis*) and Buff-breasted (*Tryngites subruficollis*) sandpipers in Argentina, and the Sanderling (*Calidris alba*) in California, switching opportunistically to other species as circumstances permitted. In addition we draw upon many field seasons with breeding and migrating shorebirds along the arctic coast of Alaska.

Territorial non-breeding shorebirds obtain control of resources within a defended area through aggressive spatial defense. In many cases an individual gains exclusive use of the area; in others, however, it does not exclude all intruders successfully. The defended site is usually fixed, with persistent boundaries that are defined by referents external to the aggressing bird. In both these respects territorial wintering shorebirds meet the most stringent criteria for territorial behavior (Noble 1939, Pitelka 1959, Wilson 1975). But they also deviate from its classic form. In fact, individual variability is so common in such central characteristics of winter shorebird territoriality as size of territory, duration and consistency of defense, dependence on territorial resources, etc., that the variation itself must be acknowledged as an essential feature of the spacing pattern. As will become evident below, the variation also serves as a useful tool for dissecting the possible benefits or costs of territorial behavior. Through this review, therefore, we will emphasize not only the characteristics of winter territoriality but also its patterns of variation.

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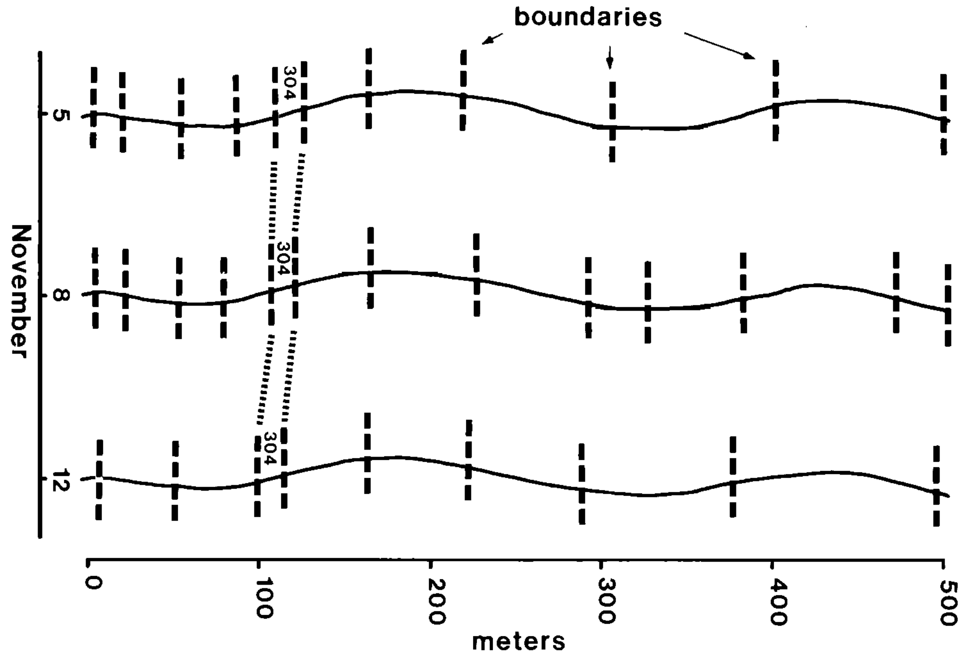

FIGURE 1. Positions of territorial boundaries defended by *Calidris alba* over 500 m of outer beach transect near Bodega Bay, California, on three days during early November 1976. Number 304 is a color-banded bird territorial on the transect during November.

FEATURES OF SHOREBIRD NON-BREEDING TERRITORIALITY

Territory Stability

Most shorebird territories have well-defined boundaries about which border fights occur regularly. After watching a series of interactions between neighbors at a border, an observer can often predict with considerable accuracy when subsequent fights will occur, based on distance of the birds from the boundary. The site-specific nature of this behavior emphasizes an important distinction between territoriality and other forms of aggression: it is controlled by external referents, obviously in response to intruders violating an externally defined space rather than individual distance.

Boundaries are often so precisely and consistently defended for periods of several days or more that they take on an almost palpable quality. Hamilton (1959), for example, found boundary positions while working with migrant Pectoral Sandpipers (*Calidris melanotos*) in Manitoba that shifted less than 10 cm per day. We have similar observations for White-rumped and Buff-breasted sandpipers and Sanderlings. But territorial arrays can also be more fluid. Figure 1 illustrates the range in boundary stability of an array of Sanderling territories along a beach near Bodega Bay, California. One bird, No. 304, was banded; as the figure shows, its territory remained in the same location throughout the plotted interval, with only a few minor shifts in border position. The constancy shown

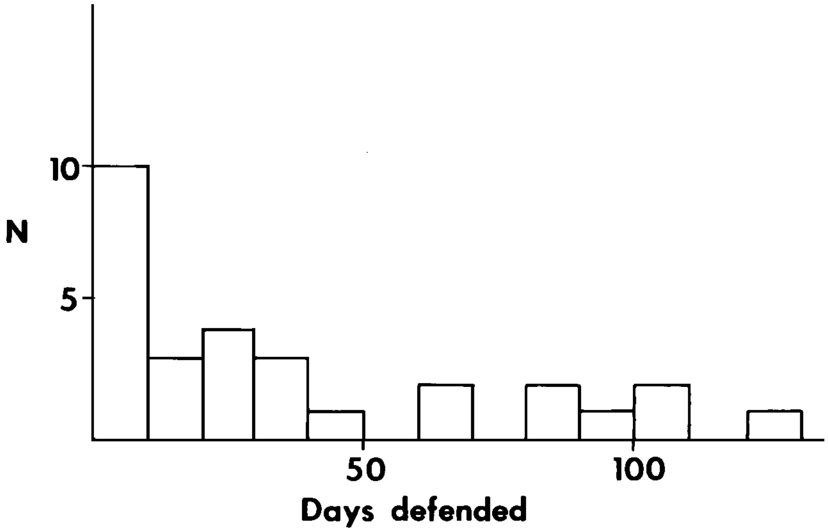

FIGURE 2. Minimum length of time in days that 31 territories were defended by color-banded *Calidris alba* on an outer beach near Bodega Bay, California, 1 October 1976 to 1 April 1977. Three individuals who switched territories at different times during the winter are treated as independent cases of defense for each site defended. All other individuals occupied only one territory per bird.

by many other boundaries on either side of No. 304 implies that other, unmarked birds remained consistent as well. Although this map suggests considerable stability in the array, some boundaries did change, shifting along the beach, disappearing entirely, or appearing de novo during the 8-day census period.

As an extreme example of shifting border position, Sanderlings also may defend an area around a foraging Black Turnstone, *Arenaria melanocephala* (Connors 1976). Occasionally a Sanderling will feed in close association with a Turnstone, working through substrate exposed by the Turnstone as it flips over beach litter. When the Turnstone moves, so does the territorial Sanderling, as does the focus of its supplantations. It is defending, in essence, a moving territory, with its aggression cued to the Turnstone's position.

Individuals vary with respect to the length of time that they defend a given territory. While some occupy sites for only a few hours, others will defend consistently for several months: individually color-marked White-rumped Sandpipers in Argentina defended territories up to two continuous months, with 14 holding territories for an average of 31 days (Myers 1976). Sanderlings can be even more persistent: during 1975, one remained territorial for seven months on an outer beach site near Bodega Bay (Connors 1976). In contrast, other Sanderlings at Bodega Bay switch locations, moving several hundred or more meters away and resuming defense in a new position. Still others, after maintaining territories for a period, may cease defense entirely. Figure 2 summarizes the length of time that 31 Sanderlings defended territories along the outer sandy beach at high tide. Many occuped sites for relatively short periods, with the mode lying under 10 days. A significant fraction, however, committed themselves for several weeks to the same location.

Consistent among-habitat differences suggest the importance of environmen-

TABLE 1
Calidris alba TERRITORY CHARACTERISTICS IN DIFFERENT HABITATS[a]

Habitat	N	Mean length	Range	Duration
Beach	31	41 m	12–89 m	Up to 7 months
Sand flat	5	27 m	18–31 m	Up to 2 months
Beach flood pool	25	5 m	2–10 m	1–2 hours

[a] Data from Bodega Bay and Santa Barbara, California.

tal factors in determining the length of territorial occupancy (Table 1). Birds clearly do not defend sites beyond a time when foraging is no longer possible. For example, Pectoral Sandpipers and other species using temporary vernal ponds in Argentina abandon their territories as the site dries (Myers and Myers 1979). But often the cause is less apparent: a territorial bird may stop defending a site yet continue foraging in the same location. Work in progress with Sanderlings at Bodega Bay suggests that cessation of defense relates to changing resource levels: territories may be defended over only a restricted portion of the range of resource densities encountered on a sandy beach, while nonterritorial foraging may take place under a broader set of conditions. As resource levels fluctuate, birds may respond by switching from one behavior to another. We suspect, however, that other factors such as predation and conspecific density also affect the likelihood of territorial defense (see below).

TERRITORY SIZE

Shorebird winter territories rarely approach a hectare in size (Table 2). As many shorebirds fly several kilometers between roosts and foraging sites, their defended areas are small compared with the scale of daily movements. They are also much smaller than breeding territories (Table 2). Despite their small size, individuals often confine most if not all foraging within territorial boundaries (see below).

Interspecific variation in territory size relates to body dimensions. In general, smaller species defend smaller territories. Table 3 presents ranges and means of

TABLE 2
COMPARISONS OF BREEDING VS. NON-BREEDING TERRITORY SIZE (HECTARES)

Species	Breeding	Non-breeding
Pluvialis dominica	25[a]	0.1–0.3[b]
Charadrius semipalmatus	0.03[c]	.01–.05[d]
Calidris fuscicollis	4[e]	.01–.05[b]
Calidris melanotos	1.5–10[a,f]	.01–.05[b]
Calidris alba	32[g]	.01–.1[d]
Tryngites subruficollis	0.05–3[h,i]	.01–.3[b]

[a] Myers, Shuford, and Pitelka 1978.
[b] Myers and Myers 1978.
[c] Smith 1969 (estimated from Fig. 2, p. 185).
[d] Myers, Connors and Pitelka, unpubl. data.
[e] Parmalee et al. 1968.
[f] Pitelka 1959.
[g] Parmalee 1970 (actually a maximum breeding density; territories may not have been contiguous, in which case territory size would be smaller).
[h] Pitelka, unpubl. data.
[i] Prevett and Barr 1976.

TABLE 3
LENGTHS OF WINTERING SHOREBIRD TERRITORIES ALONG LINEAR HABITATS (METERS)[a]

Species	N	Minimum	Maximum	Mean
Charadrius alexandrinus	2	70	145	108
Charadrius semipalmatus	5	16	30	20
Calidris alba	31	12	89	41
Charadrius vociferus	2	40	48	44
Pluvialis squatarola	4	80	155	125
Catoptrophorus semipalmatus	8	80	300	211

[a] Data from Bodega Bay and Santa Barbara, California.

territory lengths along linear habitats for a number of species ranked in order of increasing body weight. The relationship holds except for the Snowy Plover (*Charadrius alexandrinus*). This general pattern is consistent with empirical and theoretical treatments of other taxa (Schoener 1968, Wilson 1975), suggesting that wintering shorebirds are not immune to the energetic constraints governing territory size in many animal groups.

The area-body size relationship overlays, nevertheless, considerable intraspecific variation in territory dimensions. Part of this variability can be partitioned to among-habitat differences: for example, along the beach swash zone Sanderlings consistently defend large territories compared to sites occupied either on beach flood pools or on protected sandflats (Table 1). But even within one habitat, individuals defend areas of considerably varying dimensions. Figure 1 illustrates the variation in this regard among Sanderlings on the outer sandy beach. In fact, during each day represented in Figure 1, Sanderlings occupied sites along this stretch of beach spanning much of the range in variation we have observed throughout 3 years of fieldwork with the species.

Fluctuating resource levels contribute to the variation in territory size both within and between habitats. Ongoing work with Sanderlings and their major sandy beach invertebrate prey reveals several significant interactions between territorial behavior and prey densities: territories are more likely to be established and are smaller where prey densities are higher (Myers, Connors, and Pitelka, in prog.). But other factors complicate this relationship, in particular the recruitment of nonterritorial birds to areas of exceptional prey density and the effect this has on costs of defense (see below).

AGGRESSIVE DISPLAYS

Among non-breeding shorebirds, territorial individuals persistently attack or display toward intruders with varying degrees of subtlety, from barely perceptible motions to prolonged physical contact. The intensity of territorial aggression can reach astonishing limits. In some species, particularly plovers, body blows with wings occasionally fell the attacked bird; for example, a border fight between two Rufous-chested Dotterels (*Zonibyx modestus*) in coastal Buenos Aires, Argentina, at first appeared to end when one bird landed a powerful blow to the other's head. The latter flew a few meters away only to collapse in water. Nevertheless, after remaining there motionless for several minutes, it staggered up to return to the fray. Such anecdotes only begin to convey the intensity and persistence of territorial interactions between wintering shorebirds.

Displays used in these aggressive interactions are often highly ritualized and vary little among related species. Scolopacids use slight changes in tail, wing, and back feather position in territorial display; Hamilton's (1959) description of tail-lowering in Pectoral Sandpipers resembles postures in the White-rumped Sandpiper, Sanderling, Buff-breasted Sandpiper, Willet (*Catoptrophorus semipalmatus*), Lesser Yellowlegs (*Tringa flavipes*), and Hudsonian Godwit (*Limosa haemastica*). Species differences often feature peculiar feather patterns of individual species: White-rumped Sandpipers will raise their tail while dropping their wings, exposing the white rump; Sanderlings uncover their black alular patch in aggressive situations.

Plovers rely more on direct physical interaction and parallel border marches than do sandpipers. Border displays used by *Charadrius* and *Pluvialis* plovers as well as the Rufous-chested Dotterel often entail a drooped wing preparatory to striking. The tail is fanned and tilted slightly so that its upper surface projects toward the opponent. Neighboring plovers march repeatedly back and forth in parallel along a border in this posture, wing toward opponent drooped, back feathers slightly raised, and tail fanned.

While different in specific attributes, shorebird territorial signals reflect basically similar display requirements of a territorial bird. Their displays thus fall into four functional categories: 1) displays used during chases and supplantations; 2) displays used in combat; 3) displays used to establish and negotiate boundary position; and 4) displays used to identify the individual as territorial and to specify the spatial contingencies of aggression. The most elaborate of these, and certainly those of longest duration, are signals exchanged between neighbors over boundaries, either in establishing, repositioning, or identifying boundary position.

The mere presence of a visible bird in open habitat is, in a sense, a form of announcement. But spontaneous advertisements comparable to those used by breeding males are markedly absent on winter territories: non-breeding territorial displays do not occur without provocation. This point bears upon functional and contextual differences between breeding and non-breeding territorial activities. First, breeding birds exclude competitors while simultaneously attracting a mate. Non-breeders, on the other hand, are unencumbered by any need to secure a nesting partner, and exclude all intruders. As a result, the breeding bird's displays possess a functional duality not shared by their winter counterparts. Second, the context of the displays differs between winter and summer insofar as it is set by the density of interacting individuals (Table 2). This affects the distances over which signals must be effective and the rates at which behavioral interactions occur. Thus, announcement displays on winter territories may be lacking because of the constant proximity and visual contact of neighbors and because of the already high rate at which intruders evoke other display types. If there are costs associated with spontaneous announcements, as can be expected given time-budget restraints and predator regimes, then it is really not surprising that winter repertoires lack this type of display.

These general differences in function extend to specific details of display form: winter displays appear to be specialized for the non-breeding context of high density, constant proximity, and good visibility. Despite extensive experience with several species both in the arctic and on wintering grounds, we observe few winter signals during nesting. The converse also holds; very few species employ breeding displays in defense of non-breeding territories, even though breeding display activity does occur in winter flocks, particularly as spring migration approaches. Thus winter repertoires lack aerial displays (other than chases) or any complex vocalization. Those described above and drawn in Hamilton (1959) are among the most elaborate we have recorded.

The Buff-breasted Sandpiper deviates from this pattern by regularly employing some breeding displays on winter territories. This exception, however, may strengthen our argument because of the similarity in spatial scale between winter and breeding territory size for this species (Table 2). During the breeding season, males occupy sites in an exploded lek (Pitelka et al. 1974, Prevett and Barr 1976). They use several spontaneous displays to increase their conspicuousness to neighbors and potential mates, including a stylized flight pattern and ritualized jumping. Few of these spontaneous displays are used in the winter. Buff-breasted Sandpipers do, however, use a restricted set of wing postures in winter defense which are also employed in announcement on the breeding ground. The fact that winter encounters occur over similar distances and at comparable rates to breeding conditions may be important in allowing this shared repertoire.

For Semipalmated Plovers (*Charadrius semipalmatus*), the other species listed in Table 2 as having winter and summer territories of comparable size, the breeding data taken from Smith (1969) refer to areas used for nesting only. Most feeding occurred away from these sites. Information on the breeding display repertoire in Greenland where Smith obtained these data would be very interesting in this context. Near Barrow, Alaska, our primary arctic study area, individual Semipalmated Plovers usually occupy larger, noncontiguous territories defended with a wide-ranging display flight.

TERRITORIAL COMMITMENT

An individual bird invests time and energy into territorial defense, and in return obtains control over resources within its area. The magnitude of this territorial commitment differs among individuals, particularly with respect to the extent of dependence on territorial resources and the consistency of defense. By extent of dependence we mean the fraction of caloric intake necessary during a given time interval that is obtained on the territory. While this is difficult to assess directly, we estimate its magnitude by examining the proportion of foraging time that is spent on the territory, a quantity which shows great variation in territorial shorebirds.

In large part, cyclic environmental conditions set the daily patterns of territorial occupancy. Few if any birds spend continuous 24-hour periods on territories, as all are used within the context of a refuging system: territorial birds usually coalesce into communal roosts at night, or travel to other feeding areas when foraging on the territory is temporarily impractical. In nontidal areas, birds may defend throughout the daily foraging hours. For example, White-rumped Sandpipers fly up to several kilometers before dawn to territories in the inland wetlands of Argentina and remain until shortly after sunset (Myers 1976). Buff-breasted Sandpipers and Golden Plovers (*Pluvialis dominica*) defend territories in the Argentina Pampas grasslands throughout most of the day except for a period in mid-afternoon when they flock to local water holes (Myers and Myers, MS).

Complicated by tidal cycles, patterns of territorial occupancy in coastal areas

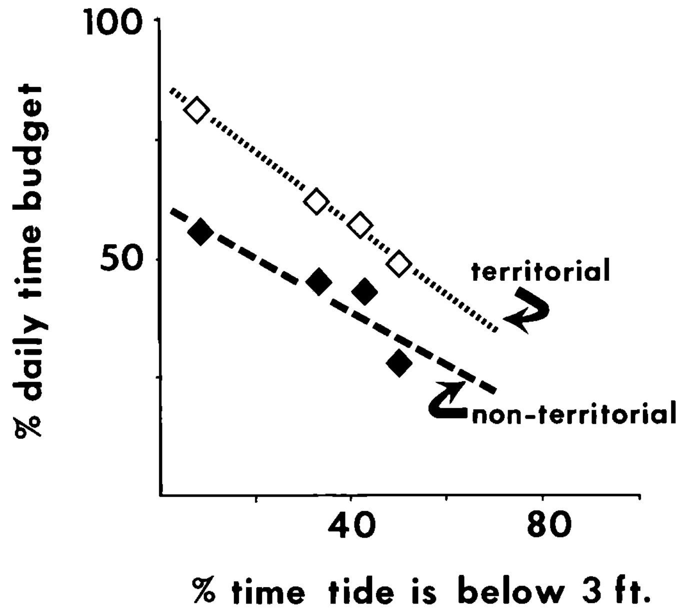

FIGURE 3. Percent daily time budget spent by *Calidris alba* on an outer beach near Bodega Bay, California, during different tidal regimes. Each point represents a separate day sampled dawn to dusk, November 1976. Percent daily time budget is a population estimate based on the maximum census obtained each sample day:

$$\% \, DTB = \frac{100}{n x_m} \sum_{i}^{n} x_i$$

where x_i = number of birds recorded during the i^{th} census; x_m = maximum census count for a given day; and n = number of censuses during a given day. Territorial and nonterritorial birds treated separately.

show far more variation. Individual birds of a few species remain on their territories during almost all tide heights. Some Willets, for example, adopt this schedule in salt marsh or along sloughs, rocky harbor shores, or on beaches. These sites share one important characteristic: they offer suitable foraging habitat over a wide range of tide heights, either because of complex ponding patterns or steep water edges with little horizontal displacement in water-line position as the tide moves out.

More commonly, a bird defends its territory during a limited period in the tidal cycle and then moves to other foraging areas as the water level changes. At similar tide heights during subsequent tidal cycles it returns to the territory. During the absence, few if any other conspecifics forage within its defended area because they too change feeding sites in response to tide levels. Sanderlings in the Bodega Bay region follow this general pattern throughout the winter. During high tides, they forage on sandy beaches, with many defending territories in fall and early winter (Fig. 1). As the tide drops, they fly to nearby harbor sandflats, moving individually or in small groups such that by low tide few remain along the beach (Connors 1976). Infrequently, individually marked birds may defend territories on the sandflats during low tides while also occupying beach territories during high tides.

Because of the relationship between foraging site and tide height, the proportion of the day spent on a territory depends upon tidal regime, i.e., the timing of tides in relation to daylight, and the relative amplitudes of high and low tide, variables which fluctuate over a lunar month. Data summarized in Figure 3 demonstrate this relationship: under all tidal conditions territorial Sanderlings devote a large proportion of their daily time budget to foraging on the territory, some individuals remaining for the entire day under appropriate tidal regimes much like the Willets mentioned above. But as the tidal regime changes and nearby sandflats lie exposed for longer periods, birds allocate less time to foraging on the beach territory (Connors, Myers, and Pitelka, in prep.). This changing pattern of use reflects but one time scale important in territorial dependence; another was examined earlier in discussing the length of time that birds remain territorial on a given site through the season.

Individuals differ both with respect to their dependence on territorial resources, as discussed above, and also in the consistency of defense. While many White-rumped Sandpipers in Argentina and Sanderlings around Bodega Bay normally respond without exception to intruders in their defended area, other individuals of these species, all color-banded, employ a behavior intermediate between classic territoriality and nonaggressive, site-specific foraging. These inconsistent birds fall into two general sets: some switch between episodes of strong defense and seemingly indifferent tolerance while others maintain a steady level of "half-hearted" supplantations, neither responding to all intruders nor cueing their behaviors as strongly to identifiable borders as do classically territorial birds. The likelihood of their aggression appears to be tied to a vaguely defined but fixed boundary zone and influenced by how close the intruder is to the resident. Their behavior thus falls between simple defense of individual distance and territoriality.

The source of this variation remains largely obscure. Individual differences based on sex or age class alone are insufficient predictors, as adult and juvenile or male and female birds all show the same range in behavior (Myers 1976, Myers, Connors, and Pitelka, in prog.). Variation in physical condition, including weight and hormonal levels, as well as past experience on the site in question may be involved. On the other hand, the consistent appearance of this ambivalent behavior in particular contexts suggests that it may be a response to environmental conditions: Sanderlings develop this pattern frequently in areas of high conspecific density while foraging on *Ulva* mats in protected sandflats or on thick mats of fresh, algal wrack along the upper beach.

Two special cases of switching between strong defense and nonaggressive tolerance can be linked directly to environmental factors: even the most consistent supplanter joins its neighbors in a compact flock when raptors fly over. Until the predator disappears, territorial aggression subsides and the flock remains together, although it may collect on an area normally defended territorially. Myers' (1976) data on dispersion in Buff-breasted Sandpipers document this clearly; territorial White-rumped Sandpipers, Sanderlings, and Golden Plovers behave similarly.

The second situation directly attributable to environmental control is seen in the response of territorial birds to invasion by a flock: while residents react at first with a burst of aggression, defense becomes sporadic and may stop if the

TABLE 4
GEOGRAPHIC RECORDS FOR TERRITORIALITY IN NON-BREEDING SHOREBIRDS

Location	Species	Source
North Slope, Alaska	*Calidris pusilla* juveniles, *Calidris melanotos*	Myers and Connors, unpub.
Manitoba, Canada	*Calidris melanotos, Calidris pusilla*	Hamilton (1959)
San Francisco Bay region, California	*Calidris mauri, Calidris alba, Catoptrophorus semipalmatus, Charadrius semipalmatus*	Recher and Recher (1969)
La Jolla, California	*Pluvialis squatarola*	Michael (1935)
U.S. Atlantic coast	*Calidris pusilla, Calidris alba*	Recher and Recher (1969)
Scotland	*Tringa totanus, Numenius arquata*	Goss-Custard (1970)
Soviet Union	*Pluvialis squatarola, Charadrius mongolus, Tringa hypoleucos, Tringa cinereus, Tringa incana, Calidris ruficollis*	Panov (1963)
Denmark	*Vanellus vanellus*	Lind (1957)

intruding group is sufficiently large (Myers, Connors, and Pitelka, in prog.). As long as the flock remains, the resident bird alternates between occasional chases and bouts of tolerant feeding. Color-marked territorial Sanderlings under these circumstances often maintain a low-intensity aggressive posture even while feeding in the flock, their tails slightly depressed and back feathers raised. We believe this pattern occurs because the flock effectively overwhelms the territory holder, increasing its defense costs beyond a supportable level. Our interpretation receives additional support from observations that if the flock disperses, spreading over several adjacent territories, the density of intruders on a given territory may fall low enough so that the resident again supplants all intruders. It will also renew consistent supplanting if the flock departs en masse. Robertson et al. (1976) interpret an interaction between schooling and territorial scarid fish similarly.

ALTERNATE STRATEGIES

The preceding discussion emphasizes a pervasive characteristic of winter shorebird spacing: a local population often contains a mixture of birds using space in different ways. Thus while up to 42% of marked local White-rumped Sandpipers foraging along a muddy stream in coastal Buenos Aires, Argentina, defended territories, the remainder of the same marked sample did not (Myers 1976). Similarly, 77 of 108 color-banded Sanderlings in Bodega Bay during the 1976–77 winter season never defended territories, while 31 did. Both Hamilton (1959) and Recher and Recher (1969) described similar patterns in other shorebirds, as did Davies (1976) for non-breeding pipits.

This heterogeneity in winter shorebird spacing must be explicitly incorporated into any analysis of their behaviors. For one, the varying extent of development of one strategy or another offers tantalizing clues as to their adaptive consequences (see below). But secondly, the very simultaneity of their expression opens an intriguing possibility: part of the payoff to birds of one behavior depends on the presence of the other and on the proportion of individuals in the

TABLE 5
OCCURRENCE OF TERRITORIALITY AMONG WINTERING SHOREBIRDS IN CENTRAL COASTAL CALIFORNIA

Species	Rocky intertidal	Sandy beach	Broad intertidal	Tidal slough, marsh	Inland wetland
Pluvialis squatarola		t	t	t	
Charadrius semipalmatus		nt	t	t	
Charadrius alexandrinus		t	nt		
Charadrius vociferous			?	t	t
Limosa fedoa		nt	nt	nt	
Numenius phaeopus	t	t			
Actites macularia	t			t	
Heteroscelus incanum	t				
Catoptrophorus semipalmatus	t	t	t	t	
Arenaria interpres			nt	nt	
Arenaria melanocephala	nt	nt	nt		
Calidris mauri			t	t	t
Calidris minutilla			nt	t	t
Calidris alpina			nt	nt	nt
Calidris canutus			nt		
Calidris alba	nt	t	t	t	
Aphriza virgata	nt				
Limnodromus griseus			nt	nt	
Percentage of species territorial	57	62	38	67	60

[a] nt indicates no territorial birds of this species seen in this habitat; t indicates that a varying proportion of individuals defend territories.

population so behaving. A simple case entails the swamping phenomenon discussed above: given that territorial birds occupy the beach, others may gain access to otherwise unavailable foraging sites by joining in a flock and overwhelming the resident (Robertson et al. 1976). Formal applications of game theory considering territorial versus nonterritorial behaviors as possible evolutionarily stable strategies (Maynard Smith 1976) may be developed profitably.

EXTENT OF SHOREBIRD NON-BREEDING TERRITORIALITY

Even though little formal attention has been directed toward shorebird nonbreeding territoriality, it has been reported from diverse geographic regions (Table 4). To these, we add records from coastal California (Table 5) and southern Argentina (Table 6). Taken together, these tables document its widespread occurrence across several continents and in many species. Among the territorial birds in both hemispheres figure representatives of many shorebird groups, including plovers, godwits, yellowlegs, and sandpipers. Of these, the charadriids and tringines are most frequently territorial: only one observed plover, the Tawny-throated Dotterel (*Oreopholus ruficollis*), never shows areal defense, while all five tringines (including *Catoptrophorus, Actitis,* and *Heteroscelus*) behave territorially.

Of 24 species commonly wintering along coastal California, we are sufficiently familiar with 18 to say that 11 of these 18 show a mixture of territorial and nonterritorial behavior (Table 5). A similar pattern holds in the coastal zone of Buenos Aires Province, Argentina, where 13 of 19 well-observed species defend territories at least occasionally (Table 6). Territorial behavior occurs regularly in all

TABLE 6

OCCURRENCE OF NON-BREEDING TERRITORIALITY IN COASTAL BUENOS AIRES PROVINCE, ARGENTINA

Species	Sandy beach	Broad intertidal	Tidal slough	Inland wetland	Upland grassland
		North American breeders			
Pluvialis dominica				t	t
Pluvialis squatarola	t	t	t		
Limosa haemastica		nt	nt	t	t
Tringa melanoleuca			t	t	
Tringa flavipes			t	t	
Calidris bairdii				t	nt
Calidris fuscicollis		nt	t	t	
Calidris melanotos				t	
Calidris alba	t	nt			
Calidris canutus	nt	nt			
Calidris himantopus			nt	nt	
Tryngites subruficollis					t
Steganopus tricolor			nt	nt	
Arenaria interpres		nt	nt		
		South American breeders			
Vanellus chilensis		nt	nt	t	?
Charadrius falklandicus	nt	nt	t	t	
Zonibyx modestus		nt	t	t	t
Oreopholus ruficollis					nt
Thinocorus rumicivorus					nt
Percentage of species territorial[a]	50	11	55	83	57

[a] *Vanellus chilensis* excluded from calculation for upland grassland.

habitats used by shorebirds in Buenos Aires Province except the broad intertidal (Table 6). This contrast emerges clearly in comparing the percentage of species territorial in each of the five habitat categories, with only 11% of species present in the broad intertidal establishing territories compared to an average of 61% in the other habitats. A χ^2 test based on the number of species territorial in each reveals significant among-habitat differences ($\chi^2 = 12.5$; $P < .03$). We have not made similar calculations for the coastal California area because our data for interior habitats are less complete.

The difference in Argentina is more striking still, because territoriality in the broad intertidal is unusual even for the one species defending mudflat sites, the Black-bellied Plover (*Pluvialis squatarola*). Elsewhere in coastal Buenos Aires, many species and many individuals defend territories; in several species the proportion of local populations behaving territorially is quite high. This is especially true with Golden Plovers and Buff-breasted Sandpipers in upland grasslands.

ADAPTIVE CONSEQUENCES

The ubiquity of non-breeding shorebird territoriality, as well as its striking features and their consistency among many species, poses a series of formidable problems: what factors influence a bird's decision to begin or cease defense? What generates the variability in individual behavior, or the population and species differences in degree of territoriality? What commitment does a bird develop to its defended area, and how long does that last? Each of these involves fundamental questions about the behavior's adaptive significance.

An early analysis of shorebird winter territoriality argued for what essentially is the null hypothesis: Hamilton (1959) concluded that territorial behavior by migrant Pectoral Sandpipers was probably both residual from breeding behavior and nonadaptive in the winter context. We reject both of these arguments: first, non-breeding territoriality cannot be residual because birds which do not hold breeding territories will defend winter territories. For example, only adult male *Calidris melanotos* or *Calidris fuscicollis* hold breeding territories (Pitelka et al. 1974), yet juvenile *melantos* as well as female and juvenile *fuscicollis* defend in the non-breeding season (Myers 1976). Female *melanotos* almost certainly do as well; one doing so simply has not yet been collected. Our observation of newly fledged Semipalmated Sandpipers (*Calidris pusilla*) fervently defending sites along the Alaskan arctic coast before their first migration further deflates the residuum hypothesis.

The second argument—that winter territoriality is nonadaptive—is more difficult to refute. If nothing else, the widespread and elaborate nature of winter territoriality stands against Hamilton's assertion. The energetic investment in establishing and maintaining territories must be considerable, as observations show that defense activities can occupy a significant portion of a territorial bird's time budget (Recher and Recher 1969, Connors 1976, Myers 1976). From what is known of the energy requirements of non-breeding shorebirds (Goss-Custard 1969) and suggested for the importance of the non-breeding period in the annual cycle of shorebird population regulation (Baker and Baker 1973), such an energy investment would be selected against were it merely nonadaptive.

Following considerations first posed by Brown (1964), we believe the key to understanding winter shorebird territoriality lies in the economics of defense. Benefits accruing to territorial behavior must be balanced with associated costs. In turn, the net profit or loss to territorial behavior has to be compared with results from a nonterritorial strategy. For the former to persist, not only must an individual be able to support its basic costs, but its behavior should also yield a more favorable balance than does nonterritoriality. Any mobile organism repeatedly faces this economic dilemma. And if the great variability in winter shorebird spacing behavior tells us anything, it is that the optimum solution changes rapidly over space and time. This general line of reasoning underlies more formal models developed by Gill and Wolf (1975) and Carpenter and MacMillen (1976) working with nectarivorous birds, although with the latter model there are also important differences.

Two sets of variables, energetic and risk, probably enter into a shorebird's benefit/cost "evaluation" of different spacing options. Their involvement is inescapable, both because of their conspicuous importance to shorebirds (Goss-Custard 1969, 1970, Page and Whitacre 1975), and because of their apparent importance in shaping spacing and social systems in general (Wilson 1975). But the relative importance of each, and the manner and direction in which they influence spacing behavior, promise to be central issues in the study of spacing patterns for some time.

Most shorebirds respond to predators by flocking, including those defending territories (Myers 1976). In light of Page and Whitacre's data on shorebird susceptibility to predators, this response appears to be highly adaptive. This suggests that the major influence of predation favors a flocking strategy: the individual should be less likely to defend a territory if by spacing out it increases its risk of predation. This increased cost of defense could, of course, be offset by increased energetic benefits accruing to the territorial bird.

Alternatively, predation might favor territoriality if shorebird antipredator strategies are hierarchically organized. In this view, the first line of defense might involve making the local area less attractive to a predator by keeping the density of conspecifics low, achieved via territoriality. This might reduce the amount of time a predator spends foraging locally. But once the predator is present, hunting in the area, the shorebird's behavior should change; the favored strategy for reducing predation risk might then be to flock together. In general, however, wintering shorebirds are not interspecifically territorial. If the principal benefit of territoriality derives from this lowered attraction of predators, advantages would accrue from eliminating other individuals of all species from the area. In fact, since winter territories are very small compared to the hunting range of avian predators, and conspecific flocks as well as other species are usually tolerated within the local area, overall shorebird densities are probably not sufficiently reduced to affect the likelihood of attracting the predator to the area. Thus from the available information we suggest that predation should be entered in the cost side of the territoriality equation.

The relevance of energetic considerations is also clear. Defense costs a bird directly because of caloric expenditures and indirectly by detracting from available foraging time. In turn, a bird presumably benefits by obtaining control over food resources within the territory, thereby reducing the rate at which competitors remove food. The ultimate payoff gained by this reduction in intruder cropping rate may derive either from short-term effects on availability of the food (e.g., Gill and Wolf 1975, Carpenter and MacMillen 1976) or long-term increases in food density or predictability (Goss-Custard, pers. comm.).

Many other variables may affect the energetic equations. In fact, the number conceivably involved is staggering, and certainly sufficiently large to produce the complex natural history we observe in shorebird winter territoriality. Several obvious candidates include food densities or dispersion (Gill and Wolf 1975, Carpenter and MacMillen 1976, Recher and Recher, 1969), resource renewal rates (Gill and Wolf 1975), intruder frequency (Schoener 1971), and the stability of local resourced through time (Horn 1968). Each may affect defensibility of a site by contributing to either costs or benefits. For example, we suspect that the last variable above figures heavily in setting the overall relationship between habitat type and dominant spacing behavior noted above. A simple case in point is the contrast between mudflats and upland grasslands: it simply does not pay to defend an area if the optimum foraging position will shift to a site 500 meters away within 30 minutes, before a bird can recoup the costs of establishing a territory. This relationship predicts that the percentage of birds territorial in tidal areas should vary with the rate of water line movement at particular sites. But it also assumes that the return on a territorial investment increases the longer that a bird can forage in the same place.

Most economic arguments, and certainly those centered around energetic considerations, assume that the payoff for non-breeding territoriality occurs within the same season. Nevertheless it is possible that a bird gains from *winter* territorial behavior because of benefits accrued during the breeding *season*. While the behavior may not be adaptive within the winter season, a bird might defend a winter site because of some effect its winter behavior has on breeding performance, such as practice in defense, early pairing, etc. Although we cannot reject this hypothesis directly, it seems improbable because of the overall similarity of winter territorial strategies between species which differ remarkably in their breeding social systems (Pitelka et al. 1974). This indicates selection for winter territoriality independent of breeding events. The nonrandom distribution of territorial behavior over habitats argues likewise. If benefits do not depend on the winter situation, but rather develop only once the bird returns to breed, why should territoriality develop in some habitats and not in others? One possibility is that even though gross benefits may not depend upon the winter environment, costs may vary between habitats, such as those differing in predation regime. Changes in the net gain would then affect the probability of behaving territorially.

Finally, we turn to a theme developed by many papers in this symposium, that of shorebird dependence on coastal wetlands and the consequences of long-term decreases in type and extent of these habitats. In a local area, shorebirds move between a variety of habitats, often in cyclic daily routines such as done by the Sanderlings at Bodega Bay. Yet their movements shouldn't be viewed as evidence for an opportunistic way of life, nor should their apparent ability to exploit several habitat types be taken to suggest a lessened dependence on any given one: their welfare undoubtedly depends upon conditions across the whole mosaic. Removing part of that system will have effects beyond the local limits of disturbance because shorebirds depend upon it as an integrated whole. Shorebirds frequently develop long-term site faithfulness to winter regions, throughout a season and year after year (Connors 1976, Elliot et al. 1976, Kelly and Cogswell, this volume, Smith and Stiles, this volume). The widespread nature of winter territoriality indicates a dependence on local resources at an even finer scale. Thus a given sector of coast supports populations relatively attached to the area and utilizing it with a spectrum of behavioral strategies finely adjusted to local conditions. Taken together, these argue for a thoughtful reconsideration of the vagility normally associated with wintering shorebirds, and in turn on the birds' abilities to adapt to adverse environmental changes. We suggest that habitat disturbance will have impacts on shorebird welfare of greater magnitude and complexity than previously suggested.

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THE ENERGETICS OF FORAGING BY REDSHANK, *TRINGA TOTANUS*

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ABSTRACT.—Redshank, *Tringa totanus,* in Britain feed in many places on the amphipod crustacean *Corophium volutator* and the polychaete worms *Nereis diversicolor* and *Nephtys hombergi.* When feeding on *Corophium,* redshank spent most time where prey density and the net rate at which they obtained energy were highest. When feeding on worms, redshank preferred the large ones and took very few small ones unless large ones were scarce. Simulation experiments with a mathematical model of the bird's feeding behavior suggested that this preference for large worms maximized the gross, and perhaps net, rate at which energy was collected. However, when *Corophium* and worms occurred together in the mud, redshank selected the amphipod even though taking worms would have enabled them to collect energy at a much greater net rate. It is unlikely that redshank selected *Corophium* for their nutrient content. The results are discussed in relation to some models of foraging by predators.

This paper summarizes the results of a field study on the selection of feeding places and prey types by redshank, *Tringa totanus,* outside the breeding season (Goss-Custard 1970, 1977a, b, c). These birds take a wide variety of prey species from estuarine flats, but in many places in Britain feed on the small amphipod crustacean *Corophium volutator* and two species of polychaete worms, *Nereis diversicolor* and *Nephtys hombergi* (Burton 1974, Goss-Custard 1969, 1977a, b, Goss-Custard, Kay and Blindell 1977, Prater 1972). The questions asked were: (i) Do redshank feed where prey is most abundant? (ii) Do redshank select between the different size classes of the same prey species? (iii) Do redshank select between the amphipod and the worms when they occur together in the mud? And (iv), if selection occurs in any of these situations, does it maximize feeding profitability, i.e., the net rate at which energy is obtained?

METHODS

Redshank were studied in a number of muddy sites on several estuaries in southern England and on the Ythan estuary in northeast Scotland. Using mainly observational techniques, I counted the numbers of small prey and worms in each of several size classes (based on the length of the bird's bill) that were swallowed per minute. By means of analyses of pellets and gizzard contents, small prey were identified and measured. The density of the various prey types in the mud was measured by standard core sampling techniques.

The preference of redshank for areas of different prey density was studied on the Ythan where the main food was *Corophium.* Five areas were marked out with stakes at different levels of a beach. The number of birds feeding in each zone was recorded when the tide was fully out during five study periods in two winters. *Corophium* density in each zone was measured during each period and related to bird density. The ranges in the values of both redshank and *Corophium* densities varied between periods. They were converted to a common scale by expressing each zone value of redshank density as a proportion of the sum total of bird densities in all zones during the period. The same procedure was applied to *Corophium* density and ingestion rate, i.e., the biomass of prey taken per minute by redshank.

The preference for prey types was studied in 30 sites in southern England. The numbers of each prey type taken were plotted against their own density in the mud. By definition, a preferred prey is one where the numbers taken depend mainly on their own density. In contrast, feeding rate on less preferred prey depends not only on their own density (few can be taken if few are present), but also on how many preferred prey are found. When the preferred prey is abundant and taken at a high

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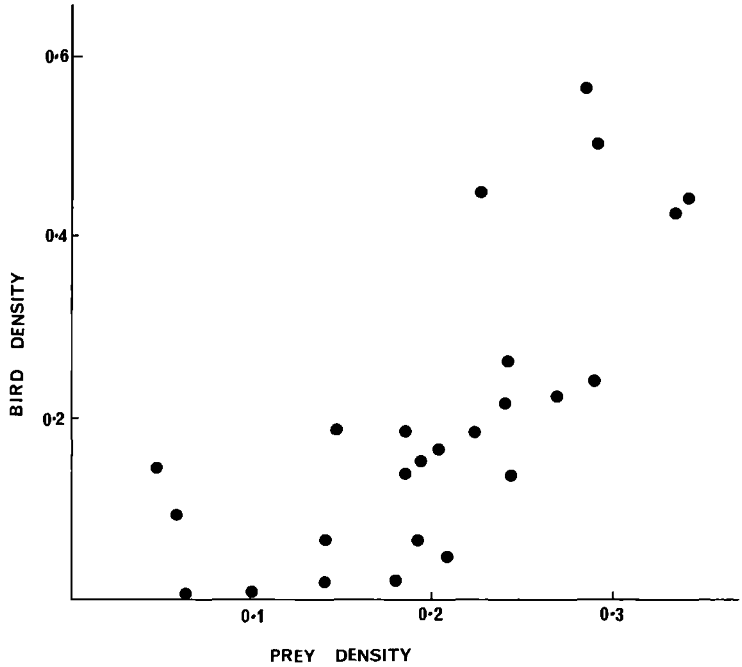

FIGURE 1. Relative density of redshank in relation to the relative density of *Corophium*.

rate, few of the less preferred ones will be taken even when they are numerous. The birds' response to the less preferred prey should be inversely related to the abundance of the preferred prey.

SELECTION FOR FEEDING PLACES

Individual redshank ranged over the whole beach but fed most where *Corophium* was densest (Fig. 1). Ingestion rate was correlated with prey density (Goss-Custard 1970, 1977c) so the birds spent most time feeding where their ingestion rate was highest (Fig. 2). Redshank also made fewer pecks and paces to collect a unit of prey biomass where *Corophium* was most abundant. Therefore, the birds preferred to feed most where they collected energy at the greatest net rate.

SELECTION BETWEEN SIZE CLASSES OF PREY

Most *Corophium* taken by redshank were over 4 mm long (maximum 10 mm) but, within this range, the numbers of small ones taken did not depend on the density of large ones (Goss-Custard 1977a). Although redshanks took more large ones than small ones overall, it is not clear whether this involved active selection or whether the birds took all they found and large ones were simply more noticeable.

The size composition of the worm populations in the different sites varied enormously and so provided a good opportunity for testing whether the birds preferred certain sizes (Goss-Custard 1977b). Using data from sites where few prey other than worms were taken, feeding rate (expressed for technical reasons as numbers taken per meter searched) on large worms (>30 mg dry weight) was quite closely correlated with their density in the mud (Fig. 3). However, the

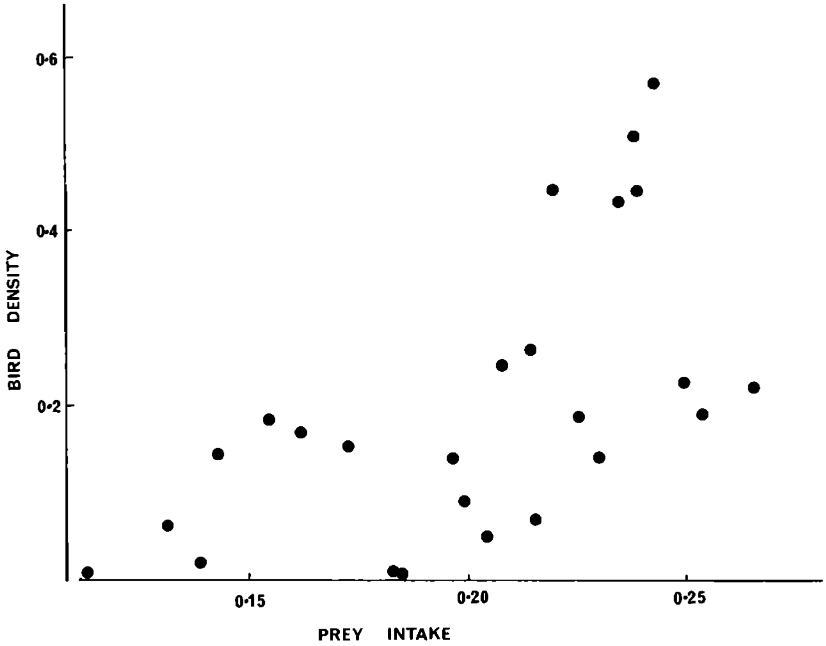

FIGURE 2. Relative density of redshank in relation to the relative rate of collecting *Corophium* biomass.

feeding rates on the medium (10–30 mg) and, particularly, small (<10 mg) ones were poorly correlated with worm densities. Feeding rate on these size classes depended more on the quantity of large worms taken because the probability that a redshank would take a small worm decreased sharply as the biomass of large

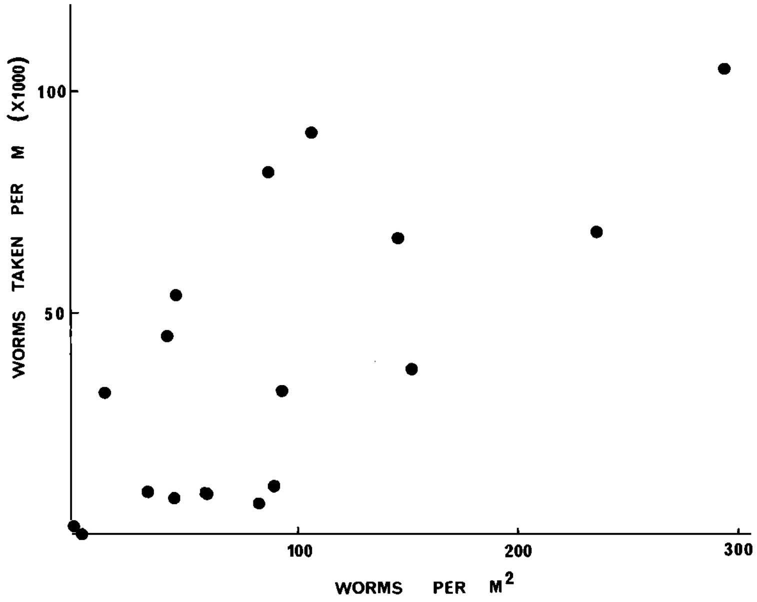

FIGURE 3. Feeding rate on large worms (>30 mg dry weight) in relation to worm density.

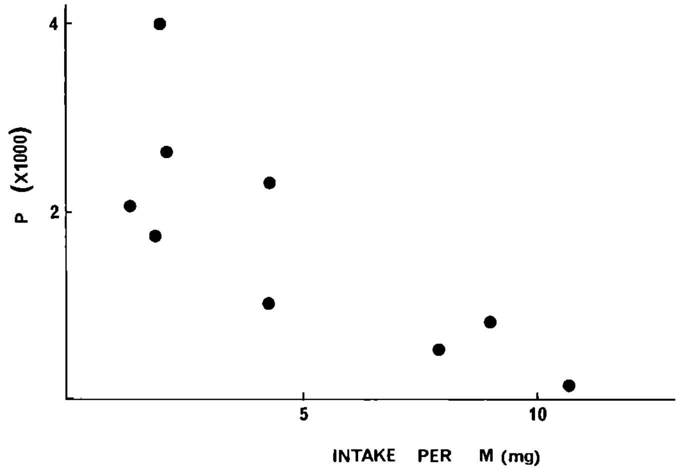

FIGURE 4. The probability (*P*) that redshank would take a small (<10 mg) worm it encountered in relation to the amount of food ingested from large worms (>10 mg). Data from sites where the density of small prey varied from 70–170 per m^2.

worms consumed increased (Fig. 4). Since the biomass intake of large worms depended on the biomass of these worms in the mud (Fig. 5), redshank were least likely to take small worms where large ones were abundant. The results suggest that redshank preferred large worms and took very few small ones unless large ones were scarce.

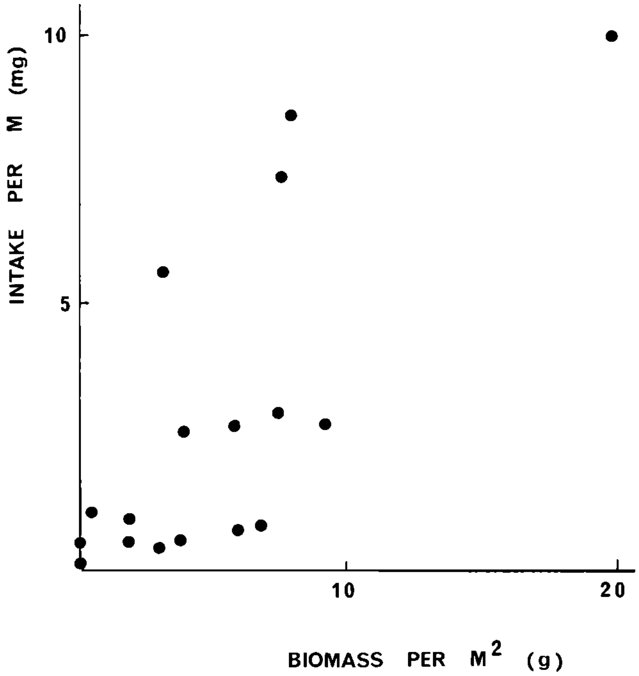

FIGURE 5. The biomass of large worms (>30 mg) taken per meter searched in relation to the biomass density of these worms in the mud.

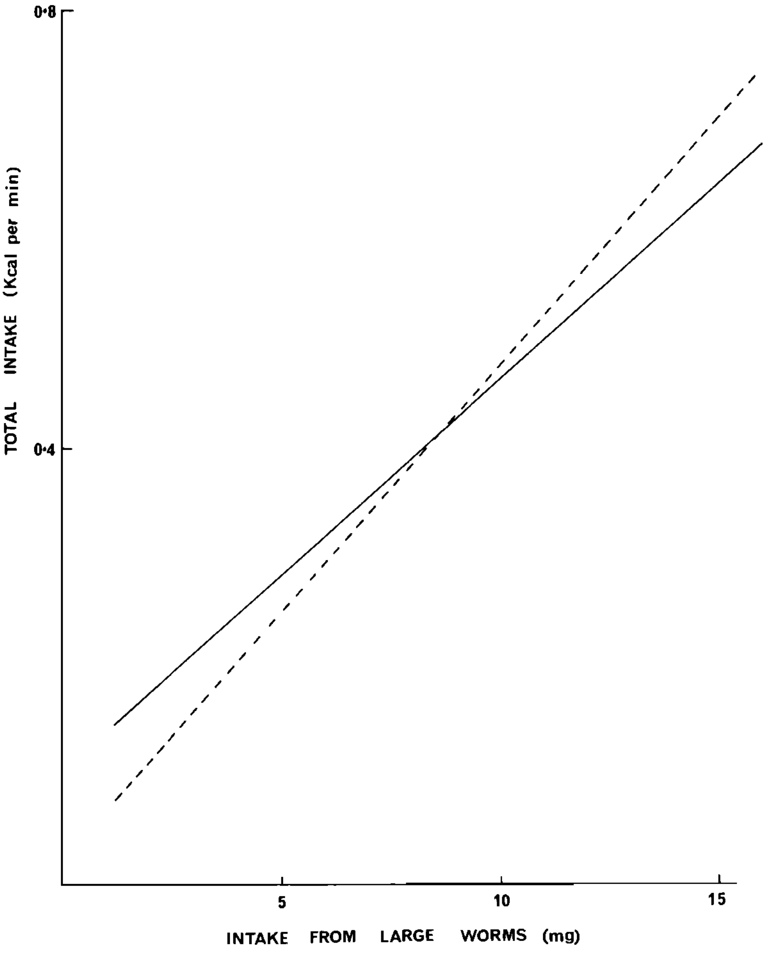

FIGURE 6. The rate of intake of energy attained by redshank taking either many (——) or a few (– – –) small worms in relation to the biomass obtained per meter from large worms. Calculated for hypothetical sites from the model.

ENERGETICS OF WORM SIZE SELECTION

This section compares the actual rates at which redshank obtained energy from worms with the potential rates obtained by selecting different sizes. Simulation experiments were carried out using a mathematical model of redshank feeding on *Nephtys* and *Nereis*. The model (Goss-Custard 1977b) consisted of a series of relationships obtained from the field data from southern England and was in two parts. First, the relationships between the numbers of each of four size classes of worms taken per meter searched and (i) their densities in the mud, and (ii) the biomass ingested per meter from larger worms, were described by regression equations. This enabled the numbers (and thence biomass) of each size class taken per meter in a particular site to be estimated from the density and mean weight of each size class in the mud. Second, the time taken per meter to search for, find and then swallow the worms of each size class was estimated from a

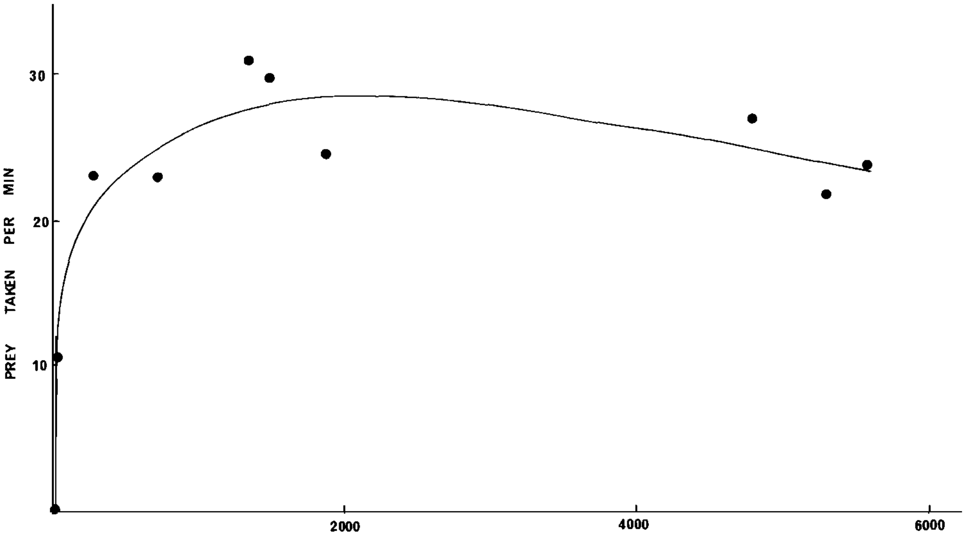

FIGURE 7. Feeding rate of redshank on small prey (mainly *Corophium*) in relation to the density of *Corophium* in the mud.

series of curves relating time expenditure on each of these activities to the size and numbers of worms taken per meter. The total biomass of worms of all sizes taken per minute, i.e., ingestion rate, was then calculated by dividing the total biomass consumed per meter by the time taken to forage that meter. Biomass intake was converted to energy intake from the calorific values of the worms.

The model was used in the following way to explore the energetics of a preference for large worms. The densities and mean weights of each size class were varied over the typical range in a series of hypothetical sites. For each site, the model gave predictions of ingestion rate for redshank feeding in the normal way. The behavior of the birds in the model was then changed as if the birds had altered their responsiveness to the small worms. In sites where large worms were numerous so the birds would actually take very few small worms, the number of small worms taken was increased by up to tenfold. The effect of this was to reduce the rate that energy was obtained from all size classes because the extra time spent stopping and taking small worms more than outweighed the extra energy obtained. In sites where large worms were scarce so the birds would actually take many small worms, the number of small ones taken was decreased by up to tenfold. Again, the effect was to reduce the overall rate at which energy was obtained because the slightly greater rate of finding large worms achieved by ignoring small ones did not compensate for the reduced amount of energy obtained from small worms.

The results are summarized in Figure 6. This compares the overall rates of energy intake achieved by two hypothetical birds feeding in a series of sites with different densities of large worms. Both birds take medium and large worms in the normal way, but one feeds by taking many small worms irrespective of the amount of large worms ingested while the other always takes very few small worms. The former approach provided the higher overall rate of intake when

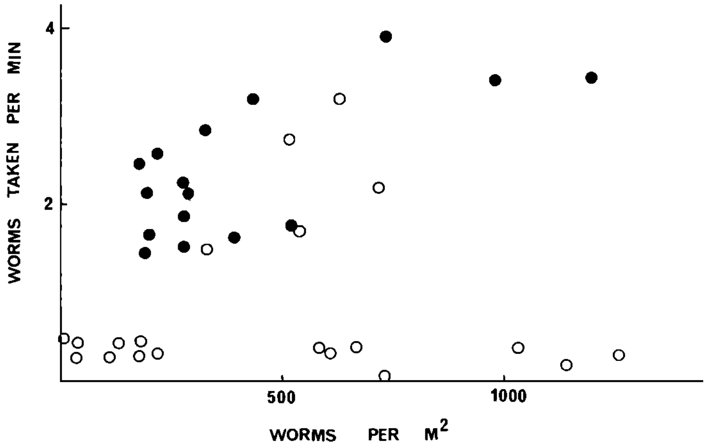

FIGURE 8. Feeding rate of redshank on worms (over 4 mg dry weight) where *Corophium* was absent (●) and present (○).

large worms are scarce but not when they are abundant. This suggests that it is more profitable for redshank to take small worms when large ones are scarce but to ignore them when large ones are numerous and this, of course, is precisely what the birds actually did. Hence it is concluded that in nature redshank took either a few or many small worms according to which was the more profitable. (Note that the results refer to gross rather than net rates of intake. The effort expended by birds behaving in the alternative ways was difficult to compare. A change from the actual to the potential response to small worms did not affect the numbers of paces and pecks made to collect a unit of energy and the time spent handling prey in similar directions. Since it is not yet possible to compare the energy expended in each of these activities, the overall effect of a change in feeding behavior on energy expenditure cannot be assessed. However, it is likely that increases in one aspect of foraging to some extent cancel out decreases in another so that the relative profitabilities of taking either many or few small worms may be similar whether expressed in gross or net terms.)

SELECTION BETWEEN PREY SPECIES

Using data from all sites, the number of small prey taken (mainly *Corophium*) was highly correlated with the density of *Corophium* in the mud (Fig. 7). Feeding rate rose rapidly but at a decelerating rate as prey density increased and then to a large extent levelled off. No site was found where *Corophium* was abundant but few were taken. This kind of Holling (1959) type-2 functional response is to be expected of a predator feeding on a preferred prey in places where prey density is uniform.

Data for feeding rates on worms produced a different pattern. Although there was a general tendency for the numbers of worms taken to increase as worm density increased, there were several sites where few were taken even though worms were very abundant (Fig. 8). This happened when *Corophium* was present because if all the sites where the amphipod occurred are excluded, there is a reasonable correlation between feeding rate and worm density. Furthermore, the

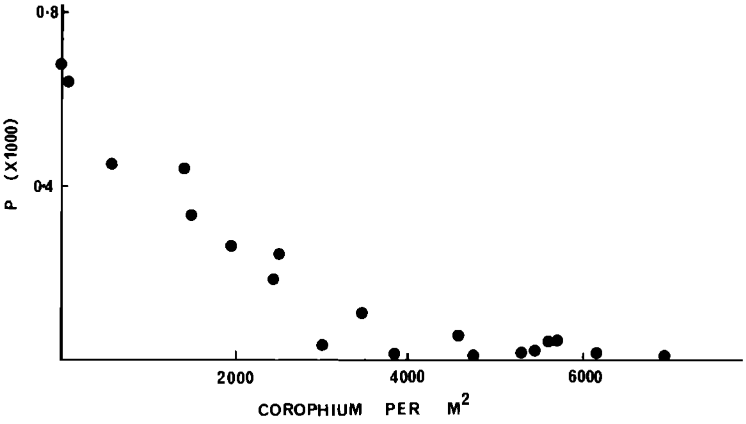

FIGURE 9. The probability (*P*) of a redshank taking a worm it encounters in relation to the density of *Corophium* in the mud.

probability that a redshank took a worm it encountered was inversely correlated with the density of *Corophium* in the mud (Fig. 9). So, rather surprisingly, it seems that the small prey *Corophium* was preferred to the much larger polychaete worms.

ENERGETICS OF PREY SPECIES SELECTION

Did taking *Corophium* yield a higher rate of energy intake than eating worms would have done? The mathematical model was used to estimate the rates of intake that would have been achieved had the birds taken worms instead. The comparison was made for the three sites in southern England where worms were abundant but the birds actually fed on *Corophium*. The values for the density and mean weight of each size class of worm recorded in each site during the sampling were put into the model and the ingestion rates calculated. The results show that, contrary to expectation, redshank would have obtained energy between two and three times faster had they taken worms rather than *Corophium* (Table 1). Table 1 also shows that birds taking worms would have made fewer pecks and paces and spent much less time in handling prey, although swallowing worms might be more costly than swallowing *Corophium*. Since the digestibilities of worms and *Corophium* are unlikely to differ enough to affect the results seriously, it appears that a preference for the amphipod did not maximise the net rate at which redshank obtained energy.

DISCUSSION

A number of authors have suggested that animals may prefer food items which can be collected most profitably (Charnov 1973, Emlen 1966, MacArthur and Pianka 1966, Pulliam 1974, Schoener 1971). By doing this, they would seem able (i) to increase their chances of collecting food at a rate sufficient for maintenance, (ii) to maximize the time spent on other essential activities, such as caring for young and avoiding predators, and (iii) to accumulate nutritional reserves for provisioning the maximum number of young. The idea has also been applied to animals choosing between alternative places in which to feed. A number of the-

TABLE 1
ACTUAL RATES OF ENERGY CONSUMPTION AND EXPENDITURE OF EFFORT BY REDSHANK FEEDING PREDOMINANTLY ON *Corophium* COMPARED WITH POTENTIAL RATES IN THE SAME SITES BUT ON WORMS

	Calories consumed per minute		Effort expended in collecting 1 Kcal: Distance searched (m)		Number of pecks		Time spent handling prey	
Site	Actual	Potential	Actual	Potential	Actual	Potential	Actual	Potential
9	88	234	103	42	470	165	62	48
10	70	224	150	44	671	167	121	49
11	93	185	106	56	543	198	79	48

oretical models have been developed which attempt to describe the behavior of animals making these choices and they have become known collectively as optimal foraging theory. The word "optimal" often leads to confusion because it appears that the models claim to portray the best means by which an animal should forage for its fitness to be maximized. Actually, an organism only needs to feed better in some sense than its competitors and there may be many considerations other than maximizing the net rate of energy or nutrient gain which contribute to its ability to do so. In fact, the models make no such claim and merely explore theoretically the various means by which an animal may make the more profitable choices while feeding. Nonetheless, to avoid confusion, it may be advisable to use alternative terms, such as profitability, which do not have the same connotations.

All the models of diet selection assume that the predator is able to assess the profitabilities associated with alternative food items. Profitability may be defined in terms of the rate of net gain of either energy or some scarce nutrient. While herbivores may often select for nutrient content, it is widely believed that carnivores are more likely to select for energy content. As Ellis et al. (1976) point out, carnivores consume food items which not only contain a wide variety of biochemical substances but are also likely to be relatively constant in nutrient composition across a variety of prey items. However, when selecting between *Corophium* and the worms, redshank took the amphipod even though feeding on worms would have enabled them to collect energy at a greater net rate. Nor is it likely that redshank selected *Corophium* for its nutrient content. The numbers of worms consumed did not depend on the biomass of *Corophium* taken (Goss-Custard 1977a) as would be expected if the birds simply took sufficient worms to make up a nutrient deficiency in their diet when *Corophium* was scarce. Therefore, it is doubtful if redshank assessed the food values of *Corophium* and worms and selected accordingly.

Although not depending on the biomass or numbers of *Corophium* consumed, the numbers of worms taken decreased markedly as the numerical density of *Corophium,* and presumably the birds' frequency of encounter with them, increased (Goss-Custard 1977a). Perhaps redshank hunt by search image (Tinbergen 1960, Dawkins 1971) and concentrate increasingly on the amphipod as its density increases. But why do they form search images for *Corophium* rather than for the worms which could be collected more profitably? One possibility is that *Corophium* is simply more noticeable and would be taken preferentially by any visually searching polyphagic shorebird that hunts by search image. However it is more likely that redshank have evolved a special sensitivity to the visual stimuli given out by *Corophium* but, if so, this also needs to be explained. No research has yet been done but perhaps a preference for *Corophium* (i) evolved as a consequence of competition with other species, (ii) provides the birds with a more widespread and dependable food source, or (iii) is associated with an evolved metabolic adaptation by redshank to different kinds of toxins or nutrients in the alternative prey species.

Although the models of profitable foraging do not predict the behavior of redshank selecting between worms and *Corophium* they predict quite well the behavior of birds choosing between alternative sizes of worms and places in which to feed. This suggests that a distinction should be drawn between the basis for selecting between some prey species and the way in which prey are exploited once they have been chosen. Having evolved a preference for *Corophium* for whatever reason, the birds' methods in exploiting it (and other prey species when forced to take them) may indeed be to choose the size classes and places in which to feed that maximize the net rate at which energy is consumed.

It is interesting that an immediate shortage of food was not required to provoke birds into choosing the more profitable means of exploiting their food niche. Redshank chose the profitably exploited prey sizes and feeding places in autumn when shorebirds appear to have little difficulty in obtaining food (Goss-Custard 1969, this volume, Heppleston 1971). Perhaps profitable foraging has a strong selective advantage when food is scarce but little disadvantage when food is abundant and so may be maintained at other times of year simply because it does not actually reduce fitness. Alternatively, there may be an advantage at all times of year in minimizing the time taken to collect energy so that more time can be spent looking for danger, for example. Again, heavy rain and strong winds can bring about a rapid deterioration in feeding conditions (Goss-Custard 1969) so that it may always be an advantage to collect energy as quickly as possible while it is available. But it is also possible that profitable foraging may simply reflect a general tendency in animals to behave economically whatever the activity, whether feeding or simply walking from place to place (Williams 1966).

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SUMMARIZING REMARKS, PART II

JOHN A. WIENS[1]

It's difficult to know where to begin in summarizing or condensing some essential truths from the preceding papers. Frank Pitelka has presented a global framework for shorebird studies, and the other speakers have added significant contributions. The edifice of knowledge of shorebird biology that emerges is incomplete, of course, but further definition of its design and structure requires new studies and fresh information, not uncertain and premature synthesis.

So saying, I could of course dismiss you all, or I could dwell at length on the spirits of some small but tasteful wineries in the valleys north of here, which I sampled as a way of preparing for this undertaking. Perhaps my hesitancy stems from my naivete about shorebird systems. After all, my own studies have been almost entirely in arid and semi-arid grasslands and deserts, which scarcely qualifies me to comment about coastal wetlands. I don't work with shorebirds. I can identify three, maybe.

It turns out, however, that the kinds of questions that are emerging in shorebird studies, as exemplified by these papers, are the same kinds of things that we have been exploring in deserts and semi-deserts, and others have been investigating in woodlands. I'm coming to the realization, however, that shorebird systems are particularly well suited to obtaining the detailed sorts of observations and conducting the innovative manipulations that are necessary to begin answering some of these questions; more so, in fact, than the sorts of systems I've been meddling with for the last decade. I'd like to draw your attention to several directions or priorities for thinking and research on shorebird systems that may be especially important, in my view.

One of these has to do with the matter of detailed dissections of behavior patterns of individuals, a topic which has received very little attention in this symposium. The paper by Shanewise and Herman on flock structure and flock behavior addressed behavior in such detail, and it indicates some interesting aspects. The size of a flock, for example, may have substantial effects upon the behavioral patterns of individuals in flocks. Regardless of whether flocking represents an adaptation to avoid predation, or to increase feeding efficiency, or both or neither of these, there is no doubt that the formation of flocks, and the foraging of individuals in large aggregations or in small flocks or as solitary birds has differing effects upon prey population dynamics in time and space. These require close attention in studies of shorebird biology.

Other studies not reported in this symposium—investigations like those of Pearson and Parker (1973) in England or Baker (1973) in North America—have used shorebirds as a system to dissect the details of behavioral patterning in time, the sequencing of movements and postures. These also indicate the utility of shorebirds for very detailed dissections of behavioral processes. They suggest that this kind of study may begin to detect something about the perceptual world of a shorebird, to unravel some of the cues that are used, for example, in prey capture, and allow us to resolve some of the facets that enter into studies of

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foraging and prey selection, such as those that Goss-Custard was just describing. We need to know how behavior is structured in time and, perhaps more importantly, what kinds of environmental influences direct the organization of behavioral sequences.

Another area involves the detailed study of foraging behavior itself and its relationship to the density and dispersion and diversity of available prey. Shorebirds are ideally suited, I think, to careful documentation and measurement of individual foraging behavior, and they occupy habitats in which prey availability and patterns can be determined perhaps more readily than in any other kind of system. Such studies ought to be related to the rich and almost exponentially growing body of optimal foraging theory, most of which remains untested. Several papers in this symposium have addressed elements of this, and I think this is an area in which shorebird studies can make fundamental contributions to the advance, or perhaps the re-direction, of a good deal of theoretical ecology. Much of the theory which is being bandied about has to do with what occurs under conditions of equilibrium and assumes that food is limited. We need to know how often this really occurs in shorebird systems. Are the birds that Goss-Custard or Hartwick and Blaylock have been working with always limited by food availability, and does this therefore impose tight constraints on what they can or cannot get away with in their foraging tactics, or may there be considerable variability or slop (what engineers call noise) in the system? Perhaps individuals may vary tremendously in their behavior without paying any real penalties. We don't know this, but I suggest that shorebird systems provide perhaps the most immediate way to begin to unravel this.

Several contributions to this symposium have alluded to energetics as an organizing framework; this is apparent, for example, in the work of Goss-Custard, of Johnson, and of Myers, Connors and Pitelka. It indicates, I think, that we need to give much closer attention to integrating energetics into large-scale ecological investigations, both in terms of energy flow in the system and in terms of the energetic options or costs/benefits that are faced by individuals or populations in pursuing particular tactics and strategies. What, for example, are the energetic consequences of the various exploitation systems documented for Arctic shorebirds by Pitelka, Holmes, and MacLean (1974)? It's apparent, however, that there may be severe difficulties in applying the rather simple energetic models that are now available to real-world situations: Johnson's demonstration of the failure of Pennycuick's (1975) model to produce reasonable estimates of flight energetics is an example—we simply can't have birds falling into the ocean this frequently. We need fresh approaches to model development that incorporate insights from biology rather than systems engineering.

Shorebird studies over the past decade or two (or three) have undergone a development which has led from an initial emphasis solely on breeding studies (perhaps as a result of the suggestions by David Lack and others that the real action must occur then, because that's when the offspring are produced) to increasing concern with what is happening on the wintering grounds. Now some are beginning to wonder what is happening to link breeding ground dynamics and wintering ground dynamics together. What happens during migration? What are the constants and the variables involved? There are some really nifty things that shorebirds can do in these wide-ranging areas that they occupy—the fixed staging areas or fixed wintering ground locations or breeding grounds. We need to explore the extent to which the so-called conservative or opportunistic adaptive strategies noted for breeding sandpipers by Pitelka and his students (1974) apply to non-breeding dynamics. Are there parallel or perhaps additional social exploitation systems that are practiced in wintering areas, or in transit along the way? What is the stability of these? What is the role or the composition of the non-breeding element of populations that occurs in some areas during the boreal breeding season?

Finally, I think we need to pay close attention to the overall stability and predictability of the systems in which these relationships occur. How variable are the environmental conditions faced by shorebirds through time and space? What role does interspecific competition play in the determination of the various population attributes that we see? How do shorebirds respond to environmental certainty or uncertainty? We have some leads in this—studies having to do with the structuring of social systems such as those of Schamel and Tracy or of Myers et al., or investigations of feeding relationships such as that of Strauch and Abele, reported on here—but this whole matter deserves intensified effort.

Obviously what's needed in order to resolve questions about the environmental relations of shorebirds and all these areas that I've only just touched upon are long-term, detailed, on-site studies that are operated within fairly well-defined theoretical frameworks, that ask questions rather than simply gather data. It is necessary to evaluate the natural patterns and magnitudes of variation in shorebird densities, distributions, behavior patterns, territorialism, non-territorialism, food habits, energetics, and so on, in order to get a fix on how these things vary under natural conditions. You can't determine how these features vary naturally by going to one area for one week and making a few observations with nothing particular in mind. It's just not that simple. What happens one year in one location may be different the next year in the same location, or the same year in a slightly different location. I think it's critical to our understanding and management of shorebird and coastal wetland systems that we undertake these long-term studies. Somehow, some way, someone has to convince the granting agencies that operating on a short-term funding frame will simply not produce the kind of science we need. It's absolutely essential that we understand the patterns and magnitudes of natural variation in these sytems if we are ever to develop a realistic approach to management. Otherwise, if we go in and disturb the system in some way, we have no idea whether the deviations from what we saw before are directly due to the disturbance that's been perpetrated on the system, or whether these simply represent natural variations tied to a variety of natural causes, which in all likelihood would have occurred anyway. The contributions to this symposium give encouraging evidence that achieving the necessary understanding is not as remote as it once seemed.

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