

ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF WHITE-FRONTED SANDPLOVERS
AND SANDERLINGS ON A SOUTH AFRICAN SANDY BEACH

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to my parents and husband for teaching me
the importance of hard work and study

to my daughter for teaching me
the importance of not doing them all the time

The White-fronted Sandplover (Charadrius marginatus)

The Sanderling (Calidris alba)



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DECLARATION

I hereby certify that this is the result of my own original investigation, except where acknowledged herein, and has not been submitted for a degree at any other university.

Signed by candidate

ABSTRACT

The dissertation comprises a general introduction, five chapters and a summary-synthesis which is designed to link the chapters into a cohesive account. Chapter 1 deals with the avian population of a southwestern Cape sandy shore and compares this population with those of sandy beaches in the eastern Cape and Natal. The abundance of birds and the estimated energy requirements of the avian populations in these three geographical areas increase during the austral summer, due to an influx of migrants from the northern hemisphere. The proportion of migrants to residents varies geographically, being greater in the southwestern Cape and Natal than in the eastern Cape. Chapter 2 summarizes information on the systematics, global distribution and morphology of two small shorebirds, the White-fronted Sandplover Charadrius marginatus and the Sanderling Calidris alba, which are identified in Chapter 1 as being dominant components of the southwestern Cape sandy shore avian population. Chapter 3 reports on the spatial and temporal use of the intertidal habitat by foraging White-fronted Sandplovers and Sanderlings. Interactions between these two species are discussed in the light of competition theory. The foraging ecology of the Sanderling and White-fronted Sandplover at Ouskip differed strikingly. Although both species exhibited a tidal cycle in foraging activities, rather than a diurnal cycle, White-fronted Sandplovers tended to feed during the latter half (i.e. mid to high tide), whereas Sanderlings fed during the first half (i.e. low to mid tide) of the tidal cycle. Both species' foraging activity also varied spatially and seasonally. White-fronted Sandplovers fed primarily in drier microhabitats above high tide level, and Sanderlings in wetter microhabitats near the water's

edge. In Chapter 4, the size and structure of Sanderling flocks are described. The frequency distribution of flock sizes of wintering Sanderlings foraging on the sandy beach at Ouskip was bimodal, with a peak at small flock sizes and another at large flock sizes. It is hypothesized that large groups of Sanderlings consist of individuals searching for subterranean prey, and that small groups consist of subsets of these larger groups which have located food patches. Chapter 5 is an analysis of breeding periodicity in White-fronted Sandplovers in southern Africa, and focuses on the relationships between geographical and year-to-year variation in breeding activity and rainfall patterns, food availability and the possible effects of competition with migrant shorebirds. This species exhibits significant geographical variation in breeding season, and significant year-to-year variation within an area which has winter (May - August) rainfall. There was no year-to-year variation in breeding season within an area with summer (November - February) rainfall.

GENERAL INTRODUCTION

Migration is an adaptation in many bird species which breed in the high Arctic and tundra. During the extended daytime period characteristic of the boreal summer in these regions, breeding migratory birds feed on a super-abundance of insects (Irving 1972). When daylength and food availability decrease, migrants move southwards to more suitable areas in which, in some instances, they outnumber resident breeding birds.

Shorebirds (Charadrii) exhibit a range of mobility, from permanent residency to migration between the northern and southern hemispheres. Therefore, comparative studies of resident and migrant shorebirds provide opportunities for examining a range of hypotheses concerning the adaptive advantages of migration. For example, Karr (1976) suggested that, in general, migrant birds rely much more on ephemerally abundant resources on their wintering grounds than do birds resident in these areas. Moreau (1966, 1972) also suggested that, in Africa, migrant shorebirds exploit food resources that are not used by residents. Moreover, he hypothesized that there is little competition for food, since the migrants have no closely related resident species. However, potential competition should not be considered only between phylogenetically closely related species, but also between species which are similar morphologically and/or ecologically (Wiens 1983). Inter-specific competition (Gause 1934; MacArthur 1972) and mutual avoidance (Morse 1974) are considered to be important factors underpinning resource partitioning (Schoener 1974). In this vein, Recher and Recher (1969) suggest that a combination of spatial and temporal segregation between wintering shorebirds minimizes inter-specific

competition. However, Burger et al. (1977) found that shorebird species overlap considerably in their diets and feeding habits.

Other studies in both the northern and southern hemispheres (e.g. Thomas & Dartnall 1971; Burger et al. 1979; Myers & Myers 1979; Myers 1980a; Myers & McCaffery 1984) interpret intra- and inter-specific aggression between shorebirds on their wintering grounds as evidence of competition. Myers (1980a) goes further, maintaining that aggressive interactions between resident breeding birds and migrants from North America have important effects on the breeding community in South America. However, other research on wintering shorebirds (e.g. Duffy et al. 1981, 1984) suggests that there is no convincing evidence of competition on shorebird wintering grounds. Despite the recent controversy concerning the utility of competition theory (Wiens 1977), there have been no long-term studies of co-existing resident and migrant shorebirds which have been aimed specifically at investigating inter-specific competition.

During the austral summer in the southwestern Cape Province of South Africa, shorebird species richness along sandy marine shores is low (Summers et al. 1977). Two species, the White-fronted Sandplover (Charadriidae: Charadrius marginatus) and the Sanderling (Scolopacidae: Calidris alba) together numerically account for about 90% of the sandy beach shorebird population (Siegfried 1981). The Sanderling is a Holarctic migrant, and is territorial on its breeding grounds (Parmelee 1970; Pienkowski & Green 1976). However, it exhibits both territorial and non-territorial behaviour on its North American wintering grounds (e.g. Burger et al. 1979; Myers & Myers 1979; Silliman et al. 1977). According to Maclean (1985), it is a non-territorial, flock-feeding species on its southern African wintering grounds.

The White-fronted Sandplover, by contrast, is a resident, territorial species with relatively solitary feeding habits (Summers & Hockey 1980; Maclean 1985). The ecology of Sanderlings has been studied in California (Myers 1980b, 1983, 1984; Myers et al. 1979, 1980, 1981; Connors et al. 1981), in England (Evans et al. 1980), along the east coast of North America (Burger et al. 1977, 1979; Walters 1984), in South America (Myers et al. 1985) and, perhaps to a lesser extent, in South Africa (McLachlan et al. 1980). Studies of White-fronted Sandplovers have, in southern Africa, addressed the species' breeding (Blaker 1966; Summers & Hockey 1980) and foraging biology (Kapp 1982).

This thesis documents some of the results of a 13-month field study of an avian population of a southwestern Cape sandy beach, focusing on the behavioural ecology of the White-fronted Sandplover and the Sanderling, and the timing of the breeding season of the White-fronted Sandplover.

The primary aims of this study were:

1. to investigate seasonal changes in the species composition and the daily energy requirements of the avian population of this sandy beach;
2. to discuss the systematics and global distributions of these species, and variation in their densities (where information is available) in order to assess how much their ranges overlap;
3. to investigate morphological similarity between White-fronted Sandplovers and Sanderlings in the light of predictions of competition theory;
4. to compare the foraging behaviour of these two species

- in terms of their spatio-temporal use of habitat, and their feeding methods;
5. to discover how any inter-specific differences in foraging behaviour, if they exist, are maintained, e.g. by competition;
 6. to suggest a foraging-related function for flocking for Sanderlings wintering in the southwestern Cape; and,
 7. to investigate whether the presence of Sanderlings has an important effect on the breeding activity of White-fronted Sandpipers in southern Africa.

Throughout this thesis I attempt, wherever possible, to interpret my results in the light of what is known about the two species outside the southwestern Cape.

The results presented herein are organized into five self-contained chapters each with its own introduction, methods, results, discussion, summary and reference sections. Chapter 5 has already been published (Crowe & Crowe 1984), and Chapters 1, 3 and 4 will be submitted for publication in due course. Although this method of presentation necessitates the duplication of some information, it expedites the communication of my results and conclusions in the scientific literature. Hopefully, Section 6, the summary-synthesis will link the preceding chapters into a cohesive 'story'.

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CHAPTER 1

THE AVIAN POPULATION OF A SANDY BEACH IN THE
SOUTHWESTERN CAPE, SOUTH AFRICA

1.1 Introduction

In the southwestern Cape Province, South Africa, the avian population of sandy marine shores differs from that of other wetland biotopes (Siegfried 1981), being characterized by a lower bird density, species richness and diversity. This is perhaps due to the fact that sandy shores are geologically and biologically highly dynamic (Brown 1964; Bally 1981). The shorebird communities of sandy beaches in the eastern Cape and Natal have been described by McLachlan et al. (1980) and Joubert (1981). Hockey et al. (1983) have conducted a preliminary broad-scale analysis of the avifaunas of southern Africa sandy shores, based on data extracted from an atlas of southern African coastal waterbirds (J. Cooper et al. in prep.). Although seasonal variation in the shorebird avifauna of rocky shores in the southwestern Cape has been described (Pringle & Cooper 1977), there is no published seasonal information for the sandy shores of this region. The aims of this study are to describe monthly variation in an avian population at Ouskip, a sandy beach in the southwestern Cape, and to compare this information with published data on seasonal variation in the avian populations of sandy beaches at Port Elizabeth (eastern Cape) and Umdloti (Natal), and with results of broad-scale atlas analyses for southern African shorebirds (Hockey et al. 1983). In these comparisons I focus on four questions:

1. Is there seasonal variation in the composition and energy requirements of the avian populations at Ouskip,

Port Elizabeth and Umdloti?

2. If there is such seasonal variation, is the pattern similar at all three localities?
3. What physical or biotic differences might ultimately cause any seasonal/geographical variation at/between these three localities?
4. Do patterns of energy requirements of sandy shore avian populations obtained from detailed seasonal counts differ from those derived from broad-scale atlas accounts?

1.2 Study areas

1.2.1 Ouskip

The Ouskip (33° 44'S, 18° 46'E) study area was a 1.5-km stretch of exposed sandy beach bounded at one end by rocky outcrops (Fig. 1.1). The environment of this beach is highly dynamic. During the study period (January 1977 - February 1978), the width of the exposed beach between the low water and high water marks of spring tides varied between 65m and 110m (Fig. 1.2). Moreover, winter storms drastically changed the slope of the beach and sand particle sizes (Fig. 1.2). Mean sea temperatures in the Ouskip area vary between 8°C during the austral summer (November - January), when upwelling is induced by southeasterly winds, and 15°C during the winter when northwesterly winds bring in oceanic water (Velimirov *et al.* 1977). A system of sand dunes extends along the beach and inland for between 50 and 500m in the area above the high water springs. Ephemeral freshwater ponds are found amongst these dunes during the winter (June - August). As with many southwestern Cape sandy beaches, Ouskip is a high-wave-energy beach (Bally 1981), and the intertidal zone is

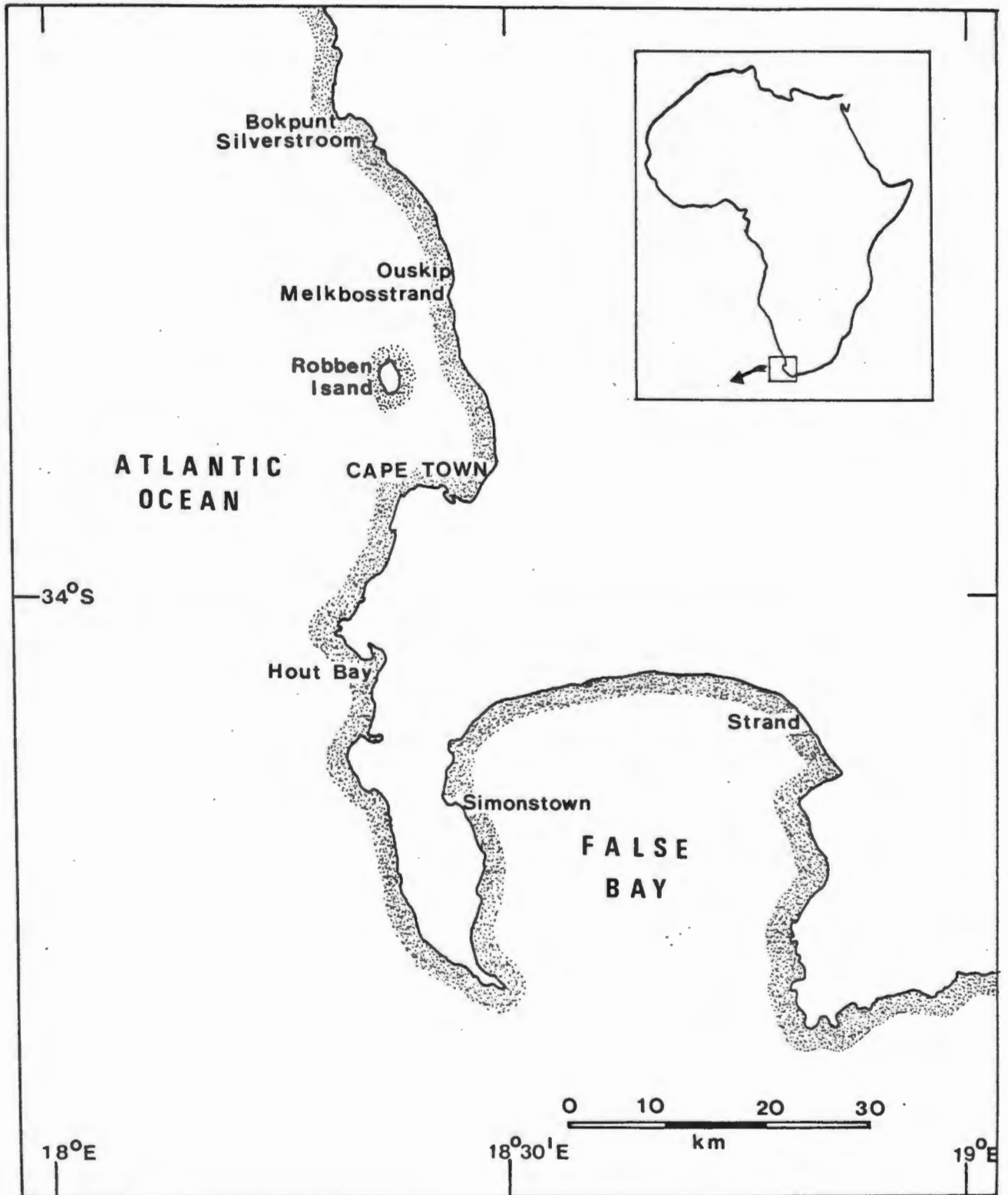


FIGURE 1.1

The southwestern Cape Province, South Africa, showing the location of the Ouskip study area

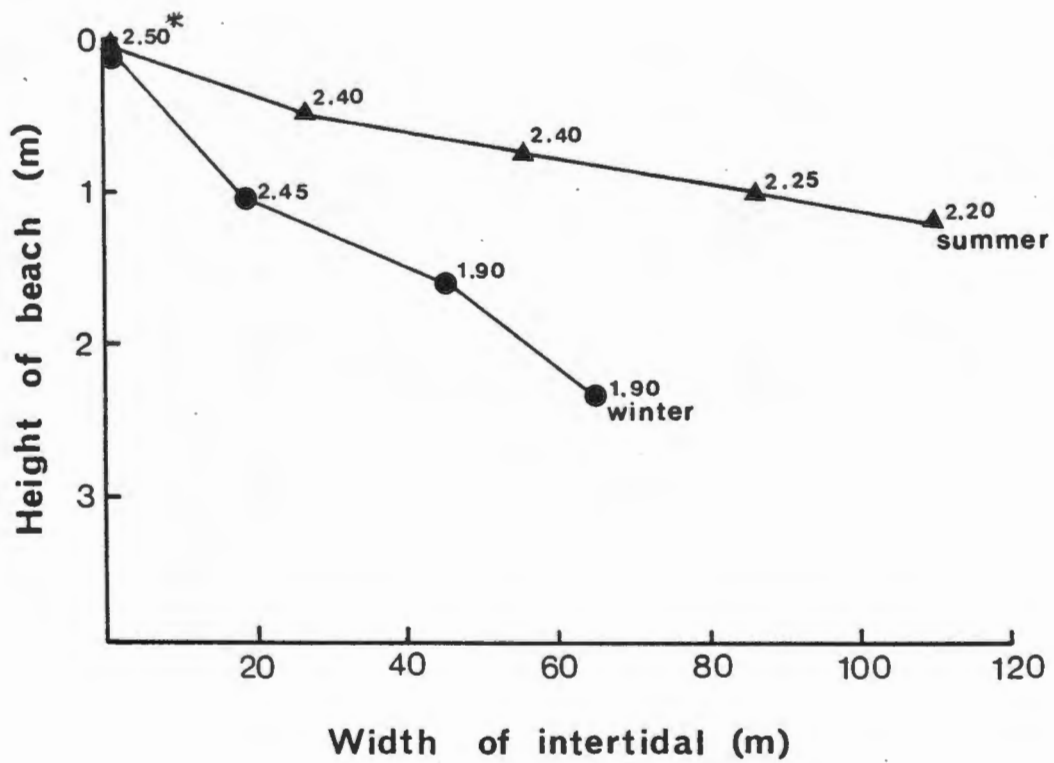


FIGURE 1.2

Profiles of the Ouskip intertidal area during summer and winter and the variation of mean sand particle size* (phi-scale) along the slope of the beach

littered with uprooted kelp from beds in the rocky sublittoral zone (Field et al. 1980). This uprooted kelp supports a rich invertebrate fauna, including species which are preyed on by shorebirds (Muir 1977; Stenton-Dozey 1983).

1.2.2 Port Elizabeth and Umdloti

The birds of three beaches in the Port Elizabeth area which were considered to be representative of the local physical and biological conditions were censused monthly by McLachlan et al. (1980). These beaches varied in their exposure ratings and in the type of dune systems which backed the upper shores of the intertidal zone. All were moderately sloping beaches, with fine- to medium-grained sand. This study area, in general, had a high standing crop of macrofauna (Table 1.1).

Although Joubert (1981) gives little information concerning the physical and biological characteristics of the Umdloti study area, he indicates that long stretches of sandy beach were interspersed with rocky outcrops, backed by low sand dunes. Data from Lawson (1982) indicate that the intertidal areas in the vicinity are steeper and have coarser sands than those at Ouskip or Port Elizabeth (Jackson & Lipschitz 1984). Natal sandy shores in general have a very low standing crop of macrofauna (Table 1.1).

1.2.3 Southern Africa

In order to summarize existing information on physical and biological characteristics of southern African sandy shores, the shore of the region was divided into 17 200-km-long segments (Fig. 1.3), similar to those recognized by Siegfried (1981) and Hockey et al. (1983). Since southern African sandy beaches vary from

TABLE 1.1
 PHYSICAL AND BIOLOGICAL CHARACTERISTICS OF SANDY BEACHES ALONG SEVENTEEN 200KM SEGMENTS
 OF THE SOUTHERN AFRICAN COAST

Coastal segment no.	Physical					Biological				
	Exposure rating a, c, d	Slope b, c, d	Sandtype b, c, d	Percentage sand e	Macrofauna -2 b, c, f, d g m	Meiofauna -2 b, c, f, d g m	Residents -1 g DEE kJ km	Migrants -1 g DEE kJ km	Shorebirds	
1				85			46		1488	
2				60			292		3733	
3				70			321		3729	
4	exposed to very exposed	moderate	medium	90	85	125	465		4706	
5	exposed to very exposed	moderate to steep	medium to coarse	65	10-1000	624	312		4879	
6				50			962	3243		
7				80			1809	5133		
8				45			1307		1370	
9				65		240	1413		2288	
10	exposed	moderate	fine to medium	60	20-7000	175	825		184	
11				35		110	527		194	
12				70		55	1151		1425	
13				80		150	597		978	
14	exposed			45	10-100	75	222		714	
15	very exposed	steep	coarse very coarse	52	20-30	100	170		169	
16				85		20	134		750	
17	exposed	moderate		90	10-90	10	186		300	

a Figure 1.1
 b McLachlan et al. (1981)
 c McLachlan (1985)
 d Bally (1981)
 e Hockey et al. (1983)
 f Koop & Griffiths (1982)
 g Daily Energy Expenditure (Walsberg 1980)

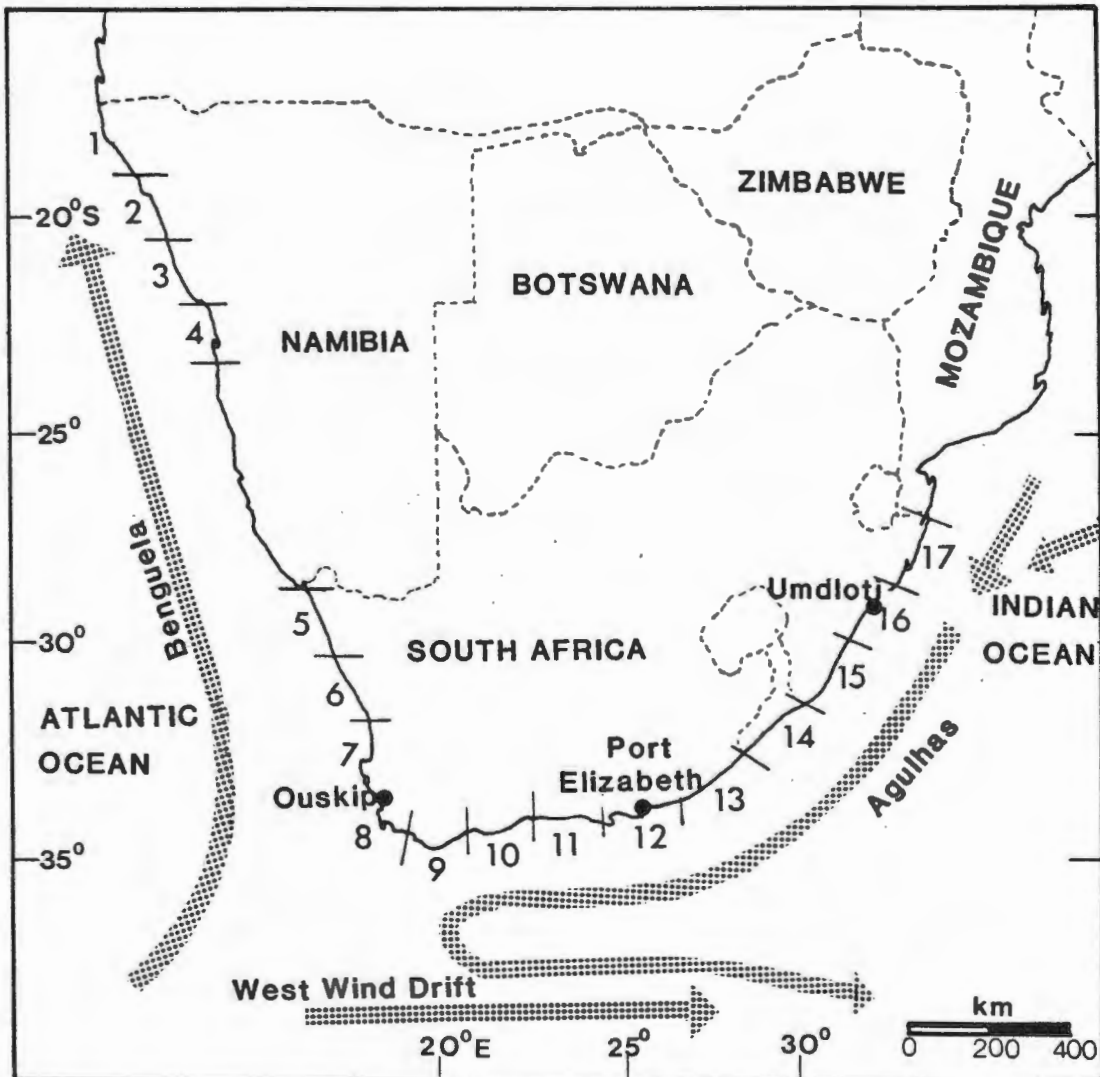


FIGURE 1.3

Southern Africa, showing the 17 200-km-long segments, used in this study, and the Ouskip, Port Elizabeth and Umdloti areas for which seasonal analyses are performed. The major ocean currents washing southern African shores are indicated

exposed to very exposed, with respect to wave action, depending on the topography of the coast, there is considerable variation in beach exposure within all segments. Moreover, the grain of sands of beaches in the west and south coasts is generally fine to medium, and that along the Transkei and Natal coasts is coarser (Table 1.1). Although the proportion of sandy to rocky shores is high along the southern Cape coast, this ratio must be interpreted with caution, since many southern Cape beaches are fragmented into small pockets of sandy and rocky beach (Jackson & Lipschitz 1984). These 'mixed beaches' are markedly different biologically from sandy and rocky beaches (Bally et al. 1984). The standing crops of intertidal macrofauna are greatest along the southwestern and southern Cape coasts (Table 1.1). The infratidal flora of these beaches also varies strikingly. East of Cape Agulhas, there are no infratidal kelp beds, and, consequently, the characteristic enormous quantities of kelp cast ashore and its associated fauna are essentially absent from beaches in the southern Cape and Natal.

The temperatures of coastal waters are affected predominantly by warm and cold current systems. The warm Mozambique Current flows southwards, passing between Africa and Madagascar. At 30° S, together with a branch of the warm South Equatorial Current, it becomes the Agulhas Current. The Agulhas Current continues to flow along the southern Cape coast, until it is deflected eastward, south of the Cape Peninsula (Brown & Jarman 1978). Some warm water from these currents may pass around the Cape of Good Hope, where it mixes with cooler west coast water from the Benguela Current (Brown & Jarman 1978). Therefore, animals which live along the coast from the Cape Peninsula eastwards to Cape Agulhas are subject to large, rapid changes in

temperature (Brown & Jarman 1978). Although sea temperature can be expected to have little direct effect on shorebird assemblages of coastal beaches, it and other abiotic variables have profound effects on the distribution and abundance of their prey (Walters 1984). Therefore, three major biogeographic zones are generally recognized for coastal southern Africa: a cool-temperate west coast zone, a warm-temperate south coast zone and a subtropical east coast zone (reviewed by Brown & Jarman 1978). The precise geographical limits of these zones, and areas of overlap, vary for different groups of organisms.

1.3 Methods

Birds at Ouskip were counted on 3-4 days per month from February 1977 to January 1978. On each day, between eight and 12 counts were made before, during and after low tide. The counts reported in this study are monthly means of number of birds per kilometre of shoreline, for each species observed in the intertidal area. The slope and width of the intertidal area were measured according to Day (1974) at spring tides. Particle size was measured along a grid at varying intertidal heights by collecting substratum samples using a plastic corer (50mm in diameter) to a depth of 60mm, and processing them using methods described by Puttick (1977).

Data on variation in the abundance of gulls (Laridae) and shorebirds (Charadrii) for the Port Elizabeth and Umdloti study areas were extracted from McLachlan et al. (1980) and Joubert (1981), and are also expressed as numbers of birds per kilometre of shoreline. Data for Little Egrets Egretta garzetta, and terns (Sternidae) were not considered, since they do not forage regularly over the sandy shore substratum.

Bird counts were converted to biomass values using mass information from Siegfried (1981). The biomass values were converted to daily energy expenditure (DEE) using Walsberg's (1980) equation. The migrant/resident ratios of the birds' energy requirements were calculated for each month for the three study areas to establish patterns of relative use by residents and migrants of the sandy intertidal. Only shorebird data were considered in these analyses to make the data comparable with those of Siegfried (1981). Cluster analysis (Field & MacFarlane 1968) was used to assess geographical variation in the austral summer energy requirements of the gull and shorebird populations between the 200km-long segments of the coast, and to determine possible seasonal variation in shorebird energy requirements within the three study areas.

1.4 Results

1.4.1 Seasonal variation in the Ouskip avian population

The bird species richness at Ouskip varied from two species during the austral winter to five species during the austral summer (Table 1.2). The Kelp Gull Larus dominicanus and the White-fronted Sandplover Charadrius marginatus were the only two species observed throughout the year. Kelp Gull numbers were greatest during March - October, and lowest during November - January. Numbers of the resident White-fronted Sandplovers were relatively constant throughout the study period. The population consisted of four pairs of territorial birds. In December, one of these pairs had a chick present on its territory, and, in January, flocks of juvenile birds occasionally visited the study area. A pair of Black Oystercatchers Haematopus moquini nested on the Ouskip beach during December - January. During the

TABLE 1.2

SEASONAL VARIATION IN THE MEAN NUMBER OF BIRDS KM OF SHORELINE AT OUSKIP (SOUTHWESTERN CAPE), PORT ELIZABETH (EASTERN CAPE) AND UMDLOTI (NATAL), THE MEAN MASS OF AND THE ESTIMATED DAILY ENERGY EXPENDITURE (DEE) OF EACH SPECIES

Species	Mean Mass (g)	DEE ^b (kJ day ⁻¹)											
		Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Residents:													
Kelp Gull (<i>Larus dominicanus</i>)	900	4.32 ^c	49.61 ^d	94.73	83.14	90.09	94.84	96.82	73.11	69.09	63.43	4.80	2.34
Greyheaded Gull (<i>Larus cirrocephalus</i>)	300	0	0	0	0	0	0	0	0	0	0	0	0
Black Oystercatcher (<i>Haematopus moquini</i>)	685	2.00	0.44	0.33	0.90	0.04	0.38	0.63	-	0.22	1.50	5.15	0.76
White-fronted Sandplover (<i>Charadrius marginatus</i>)	45	1.97	1.83	1.17	1.08	1.41	1.13	1.17	0.96	1.60	1.64	1.82	1.33
Migrants:													
Sanderling (<i>Callidris alba</i>)	55	189.94	190.15	176.35	267.24	248.43	0	0	0	20.14	28.44	98.13	125.24
Grey Plover (<i>Pluvialis squatarola</i>)	217	6.57	11.90	11.93	9.27	0.16	0.13	0	0	4.88	5.40	9.79	8.73
Curlew Sandpiper (<i>C. ferruginea</i>)	56	0	0	0	0	0	0	0	0	0	0	0	0
Knot (<i>C. canutus</i>)	143	0	0	0	0	0	0	0	0	0	3.00	1.00	0
Whimbrel (<i>Numenius phaeopus</i>)	409	0.07	0.07	0	0	0	0	0	0	0	0	0	0
Greenshank (<i>Tringa nebularia</i>)	200	0.22	0.04	0.08	0	0	0	0	0	0	0.02	0.09	0.27
Common Sandpiper (<i>T. hypoleucos</i>)	57	0	0	0	0.04	0	0	0	0	0.01	0.02	0.04	0

^a Mean mass from Siegfried (1981)

^b log DEE = log 11.87 + 0.608 log body mass (Walsberg 1980)

^c Ouskip

^d Port Elizabeth

^e Umdloti

abnormally high density due to presence of flocks of juvenile birds not 'resident' at Ouskip

austral spring and summer (September - February), the species richness and abundance of birds in the area was boosted by influxes of Sanderlings Calidris alba, and, to a much lesser extent, by Curlew Sandpipers C. ferrunginea, Knots C. canutus and Grey Plovers Pluvialis squatarola. During the austral winter (June - August), these species were either overwintering at nearby water bodies or on their northern hemisphere breeding grounds. In summer, White-fronted Sandpipers and Sanderlings accounted for more than 95% of the total number of small birds (< 100g body mass).

1.4.2 Seasonal variation in the Port Elizabeth and Umdloti avian populations

Species richness at the Port Elizabeth and Umdloti areas paralleled that at Ouskip, being low in the austral winter and higher in the summer (Table 1.2). Relative densities of Kelp Gulls, White-fronted Sandpipers and Sanderlings also showed similar patterns to those found at Ouskip, although the timing of peaks and troughs for the first two species was somewhat different. However, bird densities at Port Elizabeth and Umdloti were very much lower than at Ouskip (Table 1.2). Densities of the three dominant species (Kelp Gull, White-fronted Sandplover and Sanderling) and for all species at Port Elizabeth were about an order of magnitude lower than at Ouskip, and those at Umdloti were several times lower than at Port Elizabeth.

1.4.3 A comparison of the austral summer avian populations of segments of the southern African coast

A cluster analysis of the 17 200-km-long segments of the southern African coast, based on the summer data from the atlas

of coastal birds, suggests that there are four major avifaunal zones (I, II, III and IV in Fig. 1.4). Zone I is comprised of the one segment which extends southwards from the Cunene River in Namibia. Zone II comprises two sub-zones (i and ii). Sub-zone i consists of the remaining three Namibian segments. Sub-zone ii consists of segments 5 through 9, i.e. the southwestern Cape. Zone III comprises two sub-zones (iii and iv). Sub-zone iii consists of segments 10 - 14, i.e. the southern and eastern Cape. Sub-zone iv consists of one segment only, along the Transkei coast. Zone IV comprises two sub-zones (v and vi). Sub-zone v consists of segment 15 from southern Natal, and sub-zone vi segments 16 and 17 from central and northern Natal. These zones are not only a result of the varying species composition among the segments, but are also greatly affected by the ratio of migrant to resident shorebirds. The migrant to resident ratio decreases markedly with latitude (Fig. 1.5).

An analysis of the broad-scale atlas data shows a significant positive correlation between the resident species richness and latitude ($r = 0.52$, $P < 0.05$; Fig. 1.6C). There is no significant relationship between total species richness or migrant species richness and latitude ($r = 0.13$; $r = -0.19$, $P > 0.40$, Fig. 1.6A & B).

1.4.4 Geographical differences in energy requirements and species composition

The three study areas fall into three of the avifaunal zones recognized above (Figs 1.3 & 1.4; zones II, III and IV). The energetic demands of the avifauna (excluding gulls) of the three areas (Fig. 1.7) vary by orders of magnitude. Ouskip varies from approximately $900 \text{ kJ km}^{-1} \text{ day}^{-1}$ in winter to $32\,000+ \text{ kJ km}^{-1} \text{ day}^{-1}$

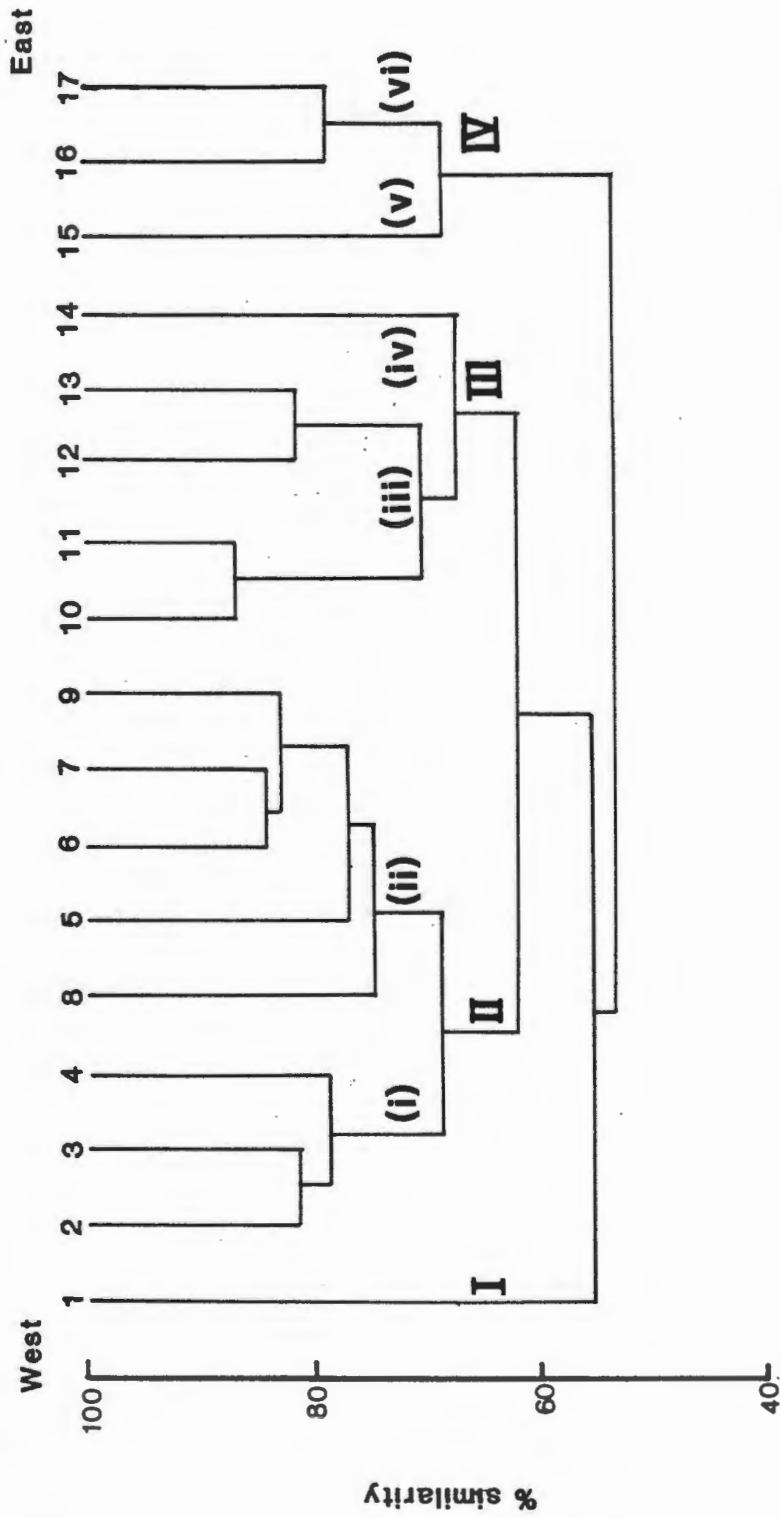


FIGURE 1.4

A comparison of 17 200-km-long segments (see Fig. 1.3) based on the energy requirements of the avian populations of sandy shores during the austral summer

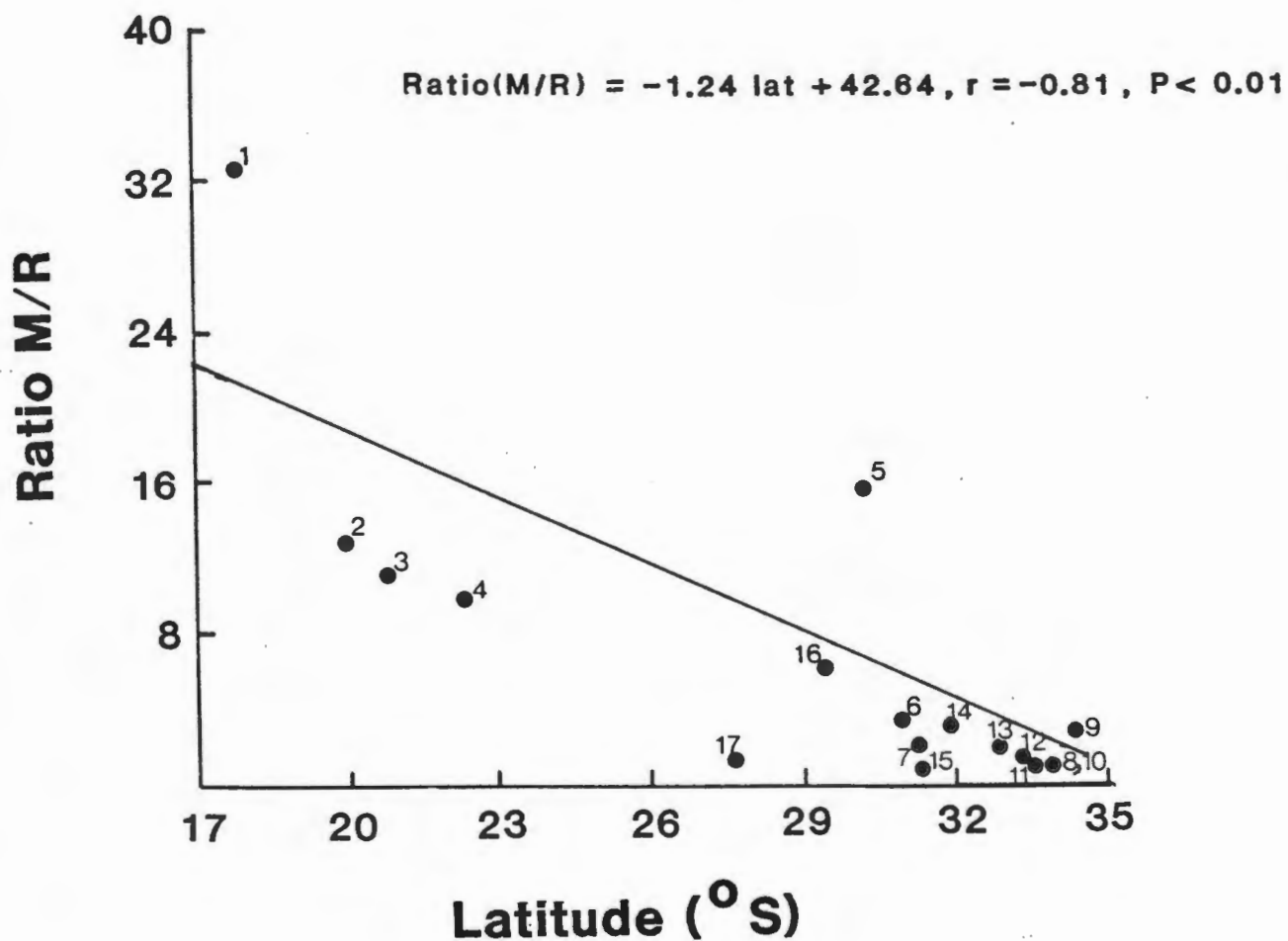


FIGURE 1.5

Energy requirements of migrant shorebirds divided by the energy requirements of resident shorebirds (excluding gulls) in relation to latitude for 17 200-km-long segments of the southern African coast (see Fig. 1.3)

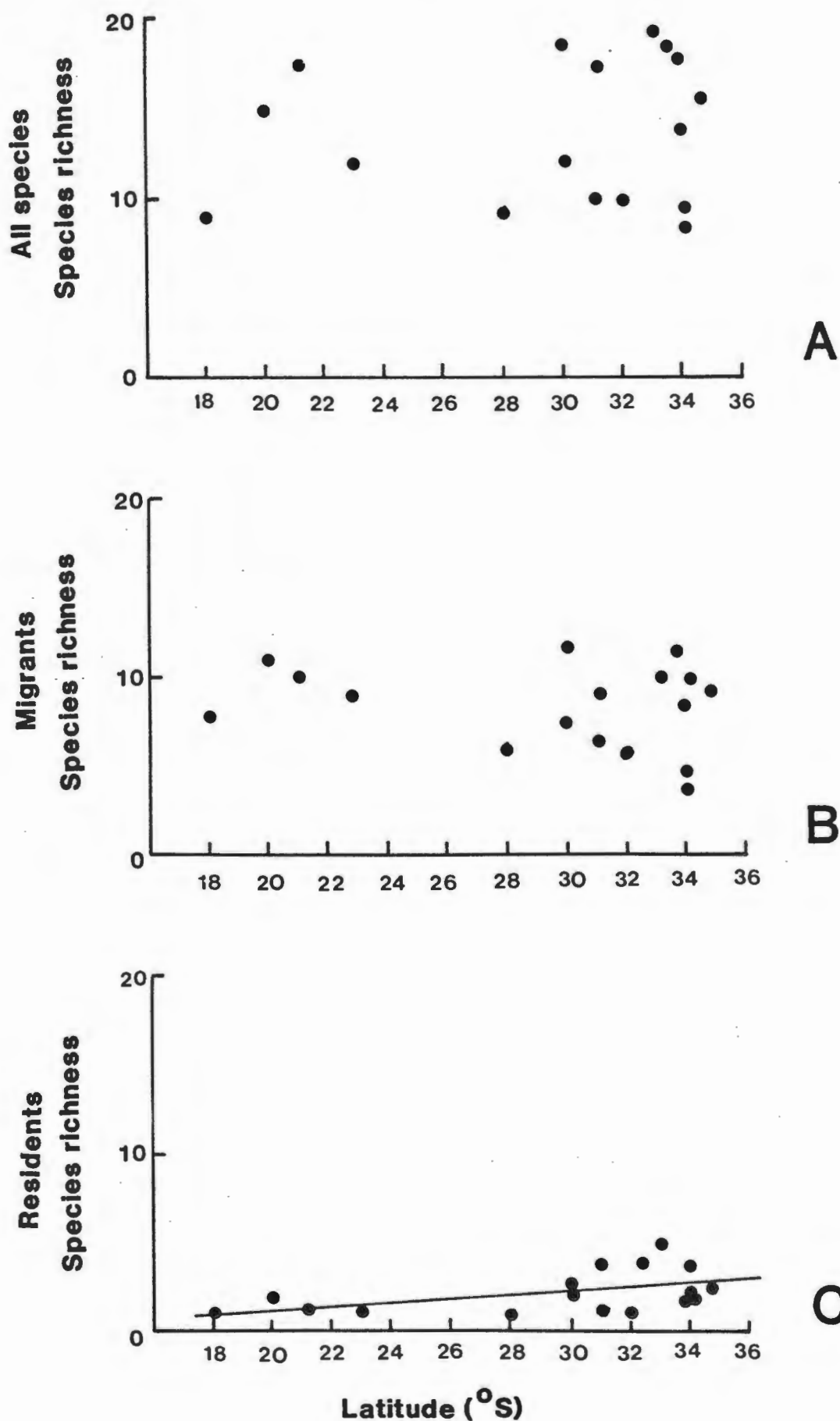


FIGURE 1.6

Avifaunal species richness and geographical latitude for segments of the southern African coast. Total species richness (A); migrant shorebirds (B); resident shorebirds (C)

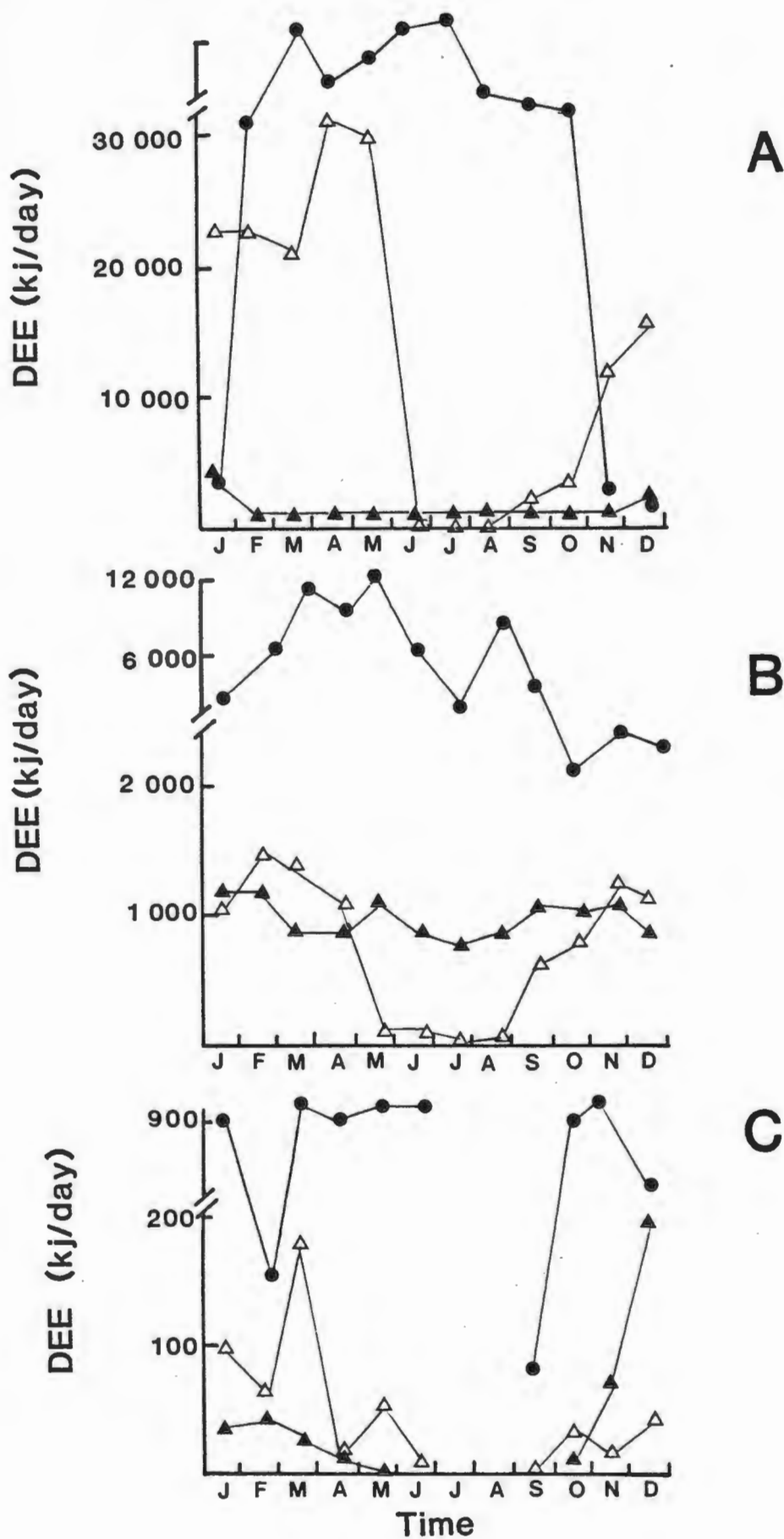


FIGURE 1.7

Seasonal variation in the energy requirements of migrant (Δ) and resident (\blacktriangle) shorebirds, and gulls (\bullet) at Ouskip (A); Port Elizabeth (B) and Umdloti (C)

in summer; Port Elizabeth from 850 to 2 800 kJ km⁻¹ day⁻¹ and Umdloti from 0 to 250 kJ km⁻¹ day⁻¹. Ouskip and Port Elizabeth have distinct clusters of winter months (Fig. 1.8A, Group I; Fig. 1.8B, Group I), and summer and autumn months (Fig. 1.8A, Group II; Fig. 1.8A, Group II), Umdloti does not (Fig 1.8C). These seasonal differences are more marked at Ouskip due to a greater influx of migrants during the summer (Fig. 1.9). Patterns of species composition also differ for all three areas (Table 1.2).

1.4.5 Intensive seasonal counts versus extensive atlas accounts

With regard to resident shorebirds, analysis of atlas data, which were collected only during the austral summer, tend to give relative DEE estimates similar to those obtained from seasonal counts at Ouskip and Port Elizabeth but much higher values than those at Umdloti (Table 1.3). Atlas data also yield higher DEE estimates for migrant shorebirds at Port Elizabeth and Umdloti, and much lower estimates for Ouskip, than seasonal counts (Table 1.3). These differences are reflected in the different migrant/resident energy requirement ratios indicated in Table 1.3. Thus, ratios of DEE estimates between localities vary greatly between the intensive counts method and the extensive atlas counts.

1.5 Discussion

1.5.1 Seasonal and geographical variation in avian populations

The answers to questions 1 and 2 posed above are YES. There is seasonal variation in the shorebird avifaunas at all three study areas, and the variation shows the same general trends. This seasonal variation is due primarily to an influx of migrants from the northern hemisphere during the austral summer. The only

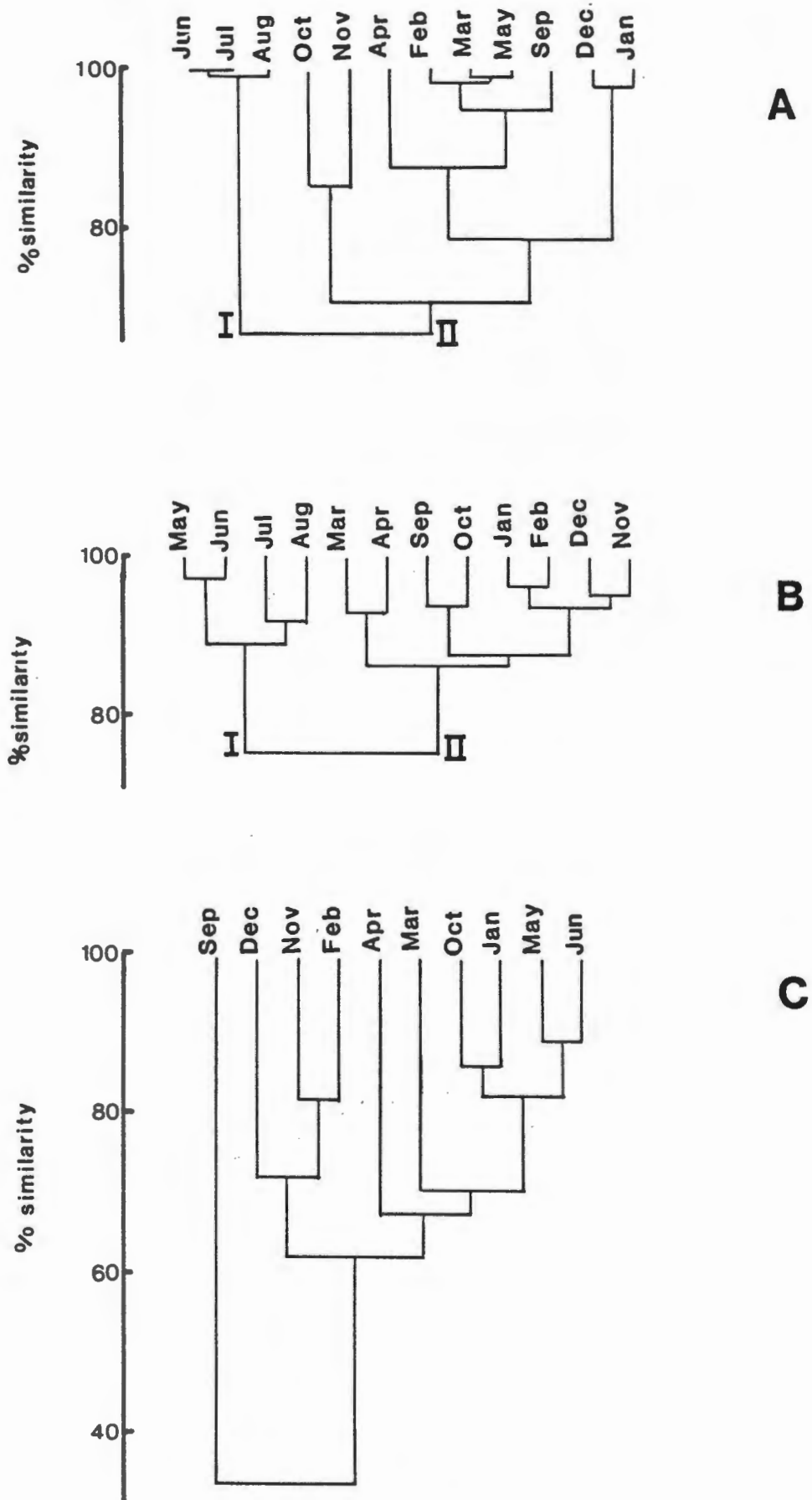


FIGURE 1.8

Seasonal comparison of the energy requirements of the sandy shore avian populations: Ouskip (A); Port Elizabeth (B) and Umdloti (C)

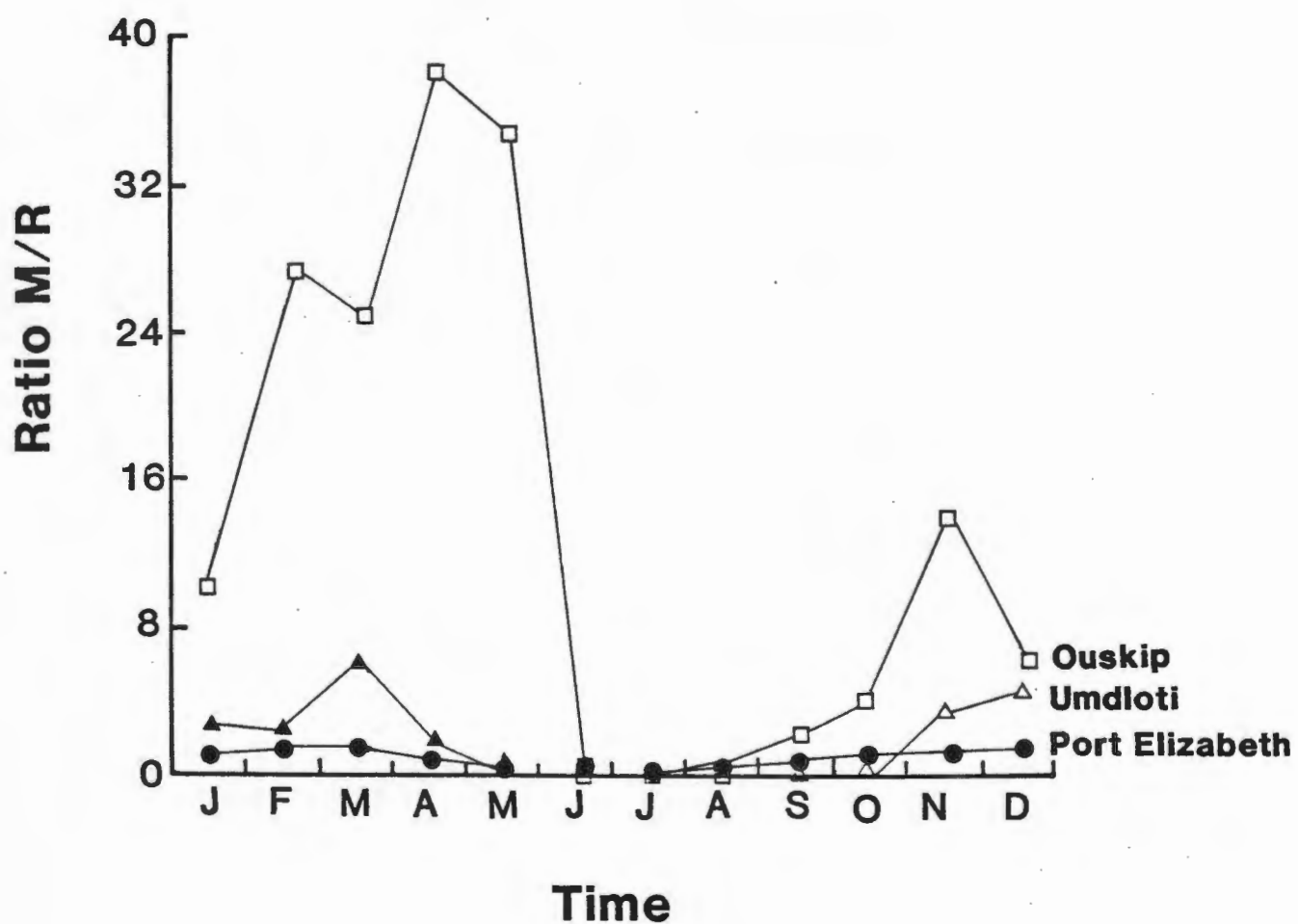


FIGURE 1.9

Energy requirements of migrant shorebirds divided by resident shorebirds (M/R) in relation to season, for Ouskip, Port Elizabeth and Umdloti

TABLE 1.3

COMPARATIVE RATIOS OF MIGRANT SHOREBIRDS, RESIDENT SHOREBIRDS AND GULLS FOR OUSKIP, PORT ELIZABETH AND NATAL, AND FOR INTENSIVE COUNTS AND EXTENSIVE ATLAS COUNTS^a, DURING THE AUSTRAL SUMMER^b

	Ouskip	Port Elizabeth	Natal	Ratio
Intensive counts:				
Migrant shorebirds	25 775 ^c *	1 088	101	255:10:1
Resident shorebirds	6 533 (2 134)	1 602	40	163:40:1 (53:40:1)
Gulls	3 206	4 209	1 704	2:2:1
Migrant/resident ratio intensive counts	4:1 (12:1)	0.7:1	3:1	
Extensive atlas counts:				
Migrant shorebirds	5 133	1 425	750	7:2:1
Resident shorebirds	1 809	1 151	134	14:9:1
Gulls	28 144	3 789	447	63:8:1
Migrant/resident ratio extensive accounts	3:1	1:1	6:1	

a

this study; McLachlan *et al.* 1980; Joubert 1981

b

Hockey *et al.* 1981

c

Estimated daily energy expenditure (DEE) (kJ day⁻¹ km⁻¹) (Walsberg 1980)

*

abnormally high value due to presence of juvenile White-fronted Sandplovers not normally 'resident' at Ouskip. Values considering resident White-fronted Sandplovers only are given in brackets

major between-site difference is in bird densities, especially those for migrant shorebirds. For example, the migrant/resident ratio of energy requirements at Ouskip in March was approximately 24.5 to 1, 7 to 1 at Umdloti and only 2 to 1 at Port Elizabeth. A certain amount of difference is also due to the breeding activities of the resident birds, e.g. influxes of immature White-fronted Sandplovers and Kelp Gulls, the departure of Kelp Gulls to breed, and to sporadic visits by Whimbrel Numenius phaeopus, Greenshank Tringa nebularia and Common Sandpiper Tringa hypoleucos to the Port Elizabeth and Umdloti study areas, and Grey-headed Gulls Larus cirrocephalus to Umdloti.

1.5.2 Causes of seasonal and geographical variation in the three sandy beach avian populations

If the differences in relative density within/between study areas are correct and reflect differences in absolute abundance (Table 1.2), there are two obvious conclusions which can be made. First, independent of season, some key shorebird resource(s) is/are in far greater supply all year round at Ouskip than at the other two study areas. Secondly, even if there is an overall superiority in resource(s) at Ouskip, during the austral summer, this resource base increases still more markedly at Ouskip than at the other two areas. I believe that the fundamental resource involved is prey. First, although the standing crop biomass values of prey at Ouskip are apparently lower than those at Port Elizabeth (Table 1.1), this is due to the fact that large beds of the White Mussel Donax serra, which are subtidal at Ouskip, are intertidal at Port Elizabeth. Interestingly, the densities of those species which prey on White Mussels (or their siphons) (e.g. the Kelp Gull, Black Oystercatcher and Sanderling) at Port

Elizabeth are not high. Secondly, kelp and the rich invertebrate fauna associated with it are absent from the Port Elizabeth and Umdloti study areas. Data on intertidal invertebrates collected at Ouskip and Dwesa (Transkei 32° 10'S, 28° 45'E) within 10 days of each other indicate that the density of potential prey is about eight times greater at Ouskip than at Dwesa (Siegfried 1977). This supports the idea of a decrease in standing crop biomass of invertebrate prey from Ouskip, through Port Elizabeth, to Umdloti. Thirdly, the availability of alternative foraging habitats is perhaps the most important contributing factor. In Chapter 3, I discuss how Sanderlings may, on a day-to-day basis, move to estuaries and other freshwater biotopes to forage. At Umdloti, this habitat switching strategy does not seem to be a viable option. In fact, species which in the southwestern Cape normally forage in alternative habitats (e.g. Common Sandpiper, Whimbrel and Greenshank) seem to be relying more on sandy beaches as their primary feeding habitat. Additional evidence in support of the use of 'alternative' habitat, and its importance as a source of food, is the fact that many first-year Holarctic migrants overwinter at estuaries in the southwestern Cape (Elliott et al. 1976; Pringle & Cooper 1977; R.W. Summers et al. in litt.). First-year Sanderlings are known to over-winter primarily at Langebaan Lagoon in the southwestern Cape (R.W. Summers et al. in litt.) with only occasional records on open beaches (Pringle & Cooper 1977). Moreover, Connors et al. (1981) have demonstrated that habitat switching by Sanderlings, also on a daily basis, is related to local variation in the productivity of food supplies. Perhaps there is similar local variation in productivity of marine shores and coastal wetlands in southern Africa.

1.5.3 Intensive seasonal counts versus extensive atlas accounts

If analyses of broad-scale atlas data, which are often based on 'once-off' counts, and those of more intensive monthly or seasonal counts yielded similar results, the sampling strategy for shorebird studies could be simplified greatly. However the results of this study suggest that they do not, and the answer to question 4 posed above is YES. Indeed, even the detailed count data analyzed in this paper also suffer from similar sources of potential sampling biases. Variation in the frequency, timing and time span of counts could result in marked differences in counts, especially those of migrants. For example, the large migrant/resident ratio at Ouskip, based on 24 to 48 counts per month, was not evident in atlas data from the same general area. Migrant/resident ratios also may have been underestimated at Port Elizabeth and Umdloti, due to less intensive counting.

Secondly, geographical variation in the foraging patterns of the species under study needs to be taken into account. Counts at Ouskip were made during the main foraging periods of birds in the intertidal area (Chapter 3). Therefore, they are presumably indicative of the birds' dependence on this shore for food. However, since monthly counts at the Port Elizabeth and Umdloti study areas were carried out only at low tide, data for Sanderlings are suspect, since Sanderlings do not forage according to a tidal cycle in this area (McLachlan et al. 1980), and little is known of their foraging behaviour at Umdloti. Also, the utility of between-year comparisons for different geographical localities should be questioned, since we know that populations of shorebirds (e.g. at Langebaan Lagoon) and of Sanderlings in southern Africa vary strikingly from year to year (Robertson 1981; R.W. Summers et al. in litt.). Last, and

perhaps most important, we need to know the degree of habitat switching for birds of the sandy shore. This must ultimately be a consequence of variation in food availability and is subject to geographical variation in the quality of alternative coastal wetlands (Begg 1984). However, data for food availability are either lacking or are not comparable due to different sampling methods.

Thus, atlas data should not be used to estimate the densities (even relative densities) of coastal birds, especially those of migrants, and migrant-resident ratios. But what of their utility in studying patterns of geographical variation in species richness of coastal birds? Diamond & Hamilton (1980), Crowe & Crowe (1982) and Guillet & Crowe (1985) have shown that such analyses are feasible for resident African birds. Although broad-scale atlas data for southern African coastal birds extend over a latitudinal range of about 15° (J. Cooper et al. in prep.), as compared with approximately 50° latitudinal data for coastal wetlands in the Americas (Pitelka 1979; Myers et al. 1985), trends in species richness of resident birds are similar in the two regions. In both areas, the number of resident breeding species is positively correlated with latitude. However, migrant bird species richness along the South American coast and along Pacific sandy shores of the Americas is negatively correlated with latitude (Pitelka 1979; Myers et al. 1985). Analyses of data for southern African coastal birds do not indicate a significant correlation between migrant shorebird species richness and latitude, although Hockey et al. (1983) report a positive correlation between shorebird species diversity and latitude. Thus, atlas data for migrant coastal birds are also probably of less value in studies of patterns of

geographical variation in species richness than are data for resident birds. Guillet & Crowe (1985) also found much lower (and non-significant) correlations between species richness of migrant waterbirds and latitude and measures of variation in the biotic and abiotic environment. I share their view that this is a result of their higher mobility and exploitation of often ephemeral flushes of food, and maintain that detailed count data which control for geographical, year-to-year, diel and tidal variation in abundance are essential for studies of coastal migrant birds. This strategy is especially crucial for dynamic biotopes such as sandy shores.

1.6 Summary

Bird species richness along a sandy beach at Ouskip during January 1977 - February 1978 varied between two species in the austral winter and five species in the austral summer. During the austral summer, migrant shorebirds from the northern hemisphere dominated the avian population numerically and in terms of its energy requirements. The large Kelp Gull and the smaller shorebirds, Sanderlings and White-fronted Sandpipers, were the only species to occur consistently in the intertidal area at Ouskip during the austral summer. Comparison between the sandy beach avian populations of study areas in the southwestern Cape (Ouskip), the eastern Cape (Port Elizabeth) and Natal (Umdloti) indicate that the overall energy requirement of the southwestern Cape population is much greater than that of the eastern Cape which, in turn, is greater than that of Natal. The relationship of these energy requirements between the resident and migrant populations varies between the three areas. The energy requirements of the migrant populations in the

southwestern Cape and Natal are much greater than those of the residents, whereas these differences are much less in the southern Cape. Comparison of these results with those of a geographically more extensive atlas data indicate that broad-scale atlas data should be used with circumspection when estimating the energy requirements of the avian populations of marine sandy shores, especially those of migrants.

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CHAPTER 2

SYSTEMATICS, DISTRIBUTION AND MORPHOLOGY OF WHITE-FRONTED
SANDPLOVERS AND SANDERLINGS

2.1 Introduction

During the austral summer, shorebird species richness along southwestern Cape marine sandy shores is low when compared with that of other wetland biotopes in the area (Siegfried 1981). Two small shorebirds, the White-fronted Sandplover Charadrius marginatus and the Sanderling Calidris alba together numerically account for about 90% of the sandy beach shorebird population in this area (Siegfried 1981; Chapter 1). Both species are more common on the notoriously dynamic (Brown 1964) sandy shores than on rocky or mixed shores during the austral summer (Summers et al. 1977). The Sanderling is a Holarctic migrant, with a polyandrous mating system and is territorial on its breeding grounds (Parmelee 1970; Pienkowski & Green 1976). However, it exhibits both territorial and non-territorial behaviour on its North and South American wintering grounds (Burger et al. 1979; Myers & Myers 1979; Silliman et al. 1977; Myers et al. 1985). It is a non-territorial flock-feeding species on its southern African wintering grounds (Maclean 1985; Chapter 4). The White-fronted Sandplover, by contrast, is a resident, monogamous, territorial species with relatively solitary feeding habits (Summers & Hockey 1980; Maclean 1985).

Inter-specific competition (Gause 1934; MacArthur 1972) and mutual avoidance (Morse 1974) have been considered important factors in resource partitioning (Schoener 1974), but they are not necessarily processes limited to phylogenetically similar species. They can in fact be operative in morphologically and/or

ecologically similar species (Wiens 1983). Baker (1977) and Burger et al. (1977) have shown that shorebirds overlap greatly in diet, and Baker (1977) concludes that other factors must be important in segregating species which forage in the same habitats. The foraging behaviour of these two species is contrasted in Chapter 3. As differences in foraging behaviour between co-existing species are often a result of morphological differences (Hespenheide 1975), it is necessary to examine those morphological variables which might affect those foraging tactics discussed in Chapter 3. Moreover, ecological as well as morphological features need to be placed in a phylogenetic context.

The aims of this chapter are:

1. to review and synthesize information on the systematics of White-fronted Sandpipers and Sanderlings;
2. to describe and discuss the global distributions of these two species;
3. to describe and discuss their relative abundance; and,
4. to compare the two species morphologically, in the light of the "character difference" (Schoener 1965) and "limiting similarity" (MacArthur & Levins 1967) theories for potentially competing or co-existing predators.

2.2 Methods

2.2.1 Systematics

The systematics of the White-fronted Sandplover and the Sanderling were reviewed and synthesized to the level of genus from information contained in Peters (1934), Bock (1958), Vaurie (1964), Clancey (1971, 1975), Johnsgard (1981) and Cramp and

Simmons (1983). The systematics of the Charadriiformes above the genus level are not clearly understood (e.g. Strauch 1978; Cracraft 1981).

2.2.2 Distribution

Abundance data for White-fronted Sandpipers and Sanderlings in southern Africa were extracted from Hockey et al. (1983) and Chapter 1, and Sanderling abundance data for North and South America from Myers et al. (1985).

2.2.3 Morphology

Seven morphological characters were measured: mass, bill length, bill width, wing length, leg length, leg width and middle toe length, on 51 White-fronted Sandpipers and 72 Sanderlings collected at Silverstroom (33° 34'S, 18° 19'E), about 40km north of Cape Town (Fig. 2.1). In addition, specimens of 144 White-fronted Sandpipers and 45 Sanderlings from the Durban, East London and Transvaal museums, were examined for the same characters. Freshly collected specimens were aged and sexed wherever possible, prior to measuring, to allow their data to be combined with those of museum specimens. Mass was recorded to the nearest gram, only on freshly collected birds with a "Pesola" balance; length of bill (mm) was measured from the tip to the proximal end of the premaxilla; bill width (mm) was measured at the proximal end of the nares; wing length (mm) refers to maximum chord (Svensson 1984); leg length (mm) refers to length of the tarsometatarsus; leg width (mm) refers to tarsometatarsus width measured halfway down the shaft and middle toe length (mm) refers to length of the third toe (Campbell & Lack 1985).

The mean values for each of the mensural characters were

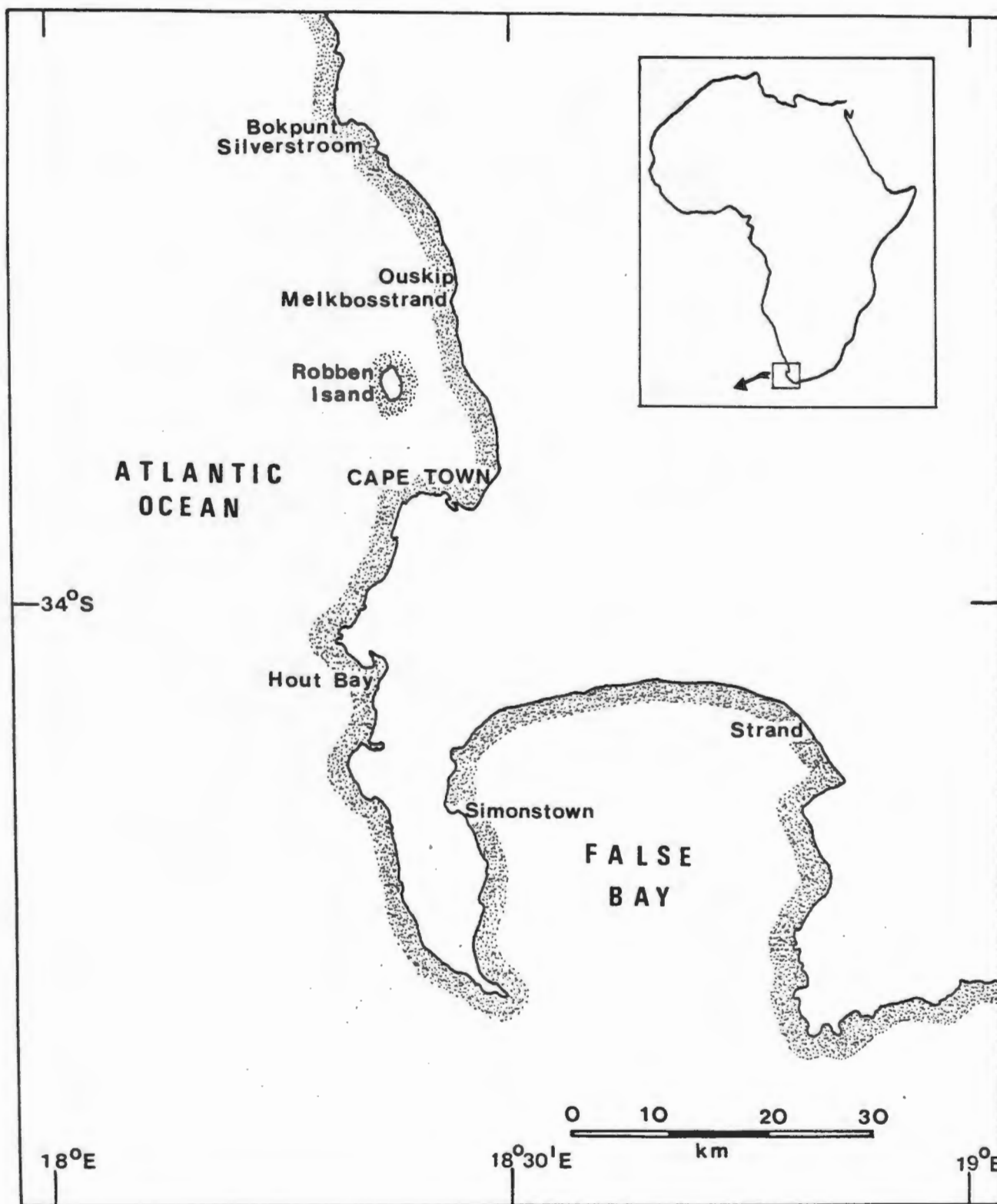


FIGURE 2.1

The southwestern Cape Province, South Africa, showing the location of the Silverstroom study area.

compared between sexes, and between species, using t-tests (Sokal & Rohlf 1981). These characters were also used in a discriminant functions analysis, BMDP7M (Dixon 1983), to identify characters important in discriminating between sexes. Discriminant functions analysis combines several morphometric variables to produce a multivariate function which maximizes a statistical separation of the sexes. This method was selected since Maron and Myers (1985) have shown that it can be used to sex Sanderlings in California. Measurements from 94 male and 80 female White-fronted Sandpipers and 39 male and 50 female Sanderlings were used in these analyses.

2.3 Results and Discussion

2.3.1 Systematics

The White-fronted Sandpiper (C. marginatus Vieillot 1818) of Afrotropics and Madagascar has often been considered conspecific with the the Kentish or Snowy Plover (C. alexandrinus Linnaeus 1758) of the Neotropics, the Palaearctic region and Asia, and the Red-capped Plover (C. ruficapillus Temminck 1821) of Australia (Peters 1934; Bock 1958). Vaurie (1964) recognizes C. ruficapillus as a monotypic species which is not conspecific with C. alexandrinus and C. marginatus. The major differences between C. alexandrinus and C. marginatus are that C. marginatus is smaller than C. alexandrinus, has a proportionally longer tail, shorter wings, weaker feet, yellowish (as opposed to black) legs, and C. alexandrinus assumes a breeding plumage, whereas C. marginatus does not. These species also differ in their breeding behaviour (Vaurie 1964; Clancey 1975).

Information concerning sympatry and reproductive isolation between these two species in western and eastern Africa where the

ranges of these two species may meet, is not available. Therefore, I follow Vaurie's (1964), Clancey's (1975) and Dowsett's (1978) reasoning, and consider the species C. alexandrinus, C. marginatus and C. ruficapillus to be allospecies of the superspecies C. alexandrinus.

Clancey (1971, 1975) recognizes 5 subspecies of C. marginatus. These subspecies differ largely in size (as reflected by wing length), ground colour of the upper parts, extent of fringing to dorsal feathering and, to a lesser extent, in bill size, amount of black on the foreheads of adult males, and the development of a white hind neck bar. The subspecies are as follows:

1. C. m. marginatus Vieillot 1818
2. C. m. arenaceus Clancey 1971
3. C. m. tennellus Hartlaub 1861
4. C. m. mechowi (Cabanis 1884)

including C. m. hesperius and C. m. nigrius Bates 1932

5. C. m. pons Neumann 1929

Since the subspecies C. m. marginatus and C. m. arenaceus exhibit very different foraging habits (Chapter 3), I suggest that the systematics of the southern African populations of this species should be re-investigated using behavioural characters and possibly juvenile plumage patterns.

Subspecies of C. alexandrinus recognised here are as follows:

1. C. a. alexandrinus Linnaeus 1758
2. C. a. dealbatus (Swinhoe 1870)
3. C. a. nivosus (Cassin 1858)
4. C. a. javanicus Chasen 1938
5. C. a. tenuirostris (Lawrence 1862)
6. C. a. occidentalis (Cabanis 1872)

7. C. a. seebohmi Hartert & Jackson 1915

The Sanderling Calidris alba (Trynnga alba Pallas 1764) has been separated by some authors (see Peters 1934) from the genus Calidris and placed in a monotypic genus Crocethia due to the absence of the hind toe. In spite of its immense wintering range and morphometric differences which appear to exist between the Greenland and Siberian breeding populations (Summers 1975; Prater & Davies 1978; R.W. Summers et al. in litt.) this species is generally considered monotypic (Peters 1934; Johnsgard 1981; Cramp & Simmons 1983). Whereas Sanderlings wintering in California appear to be indistinguishable, in the field, from Sanderlings wintering in southern Africa, their behaviour is very different (Myers 1984; Chapter 3).

2.3.2 Distribution

Charadrius alexandrinus, C. marginatus and C. ruficapillus, the three allospecies comprising the superspecies C. alexandrinus, have a global distribution (Fig. 2.2). The polytypic C. alexandrinus inhabits the west (C. a. nivosus) and south (C. a. tenuirostris) coasts of North America, the west coast of South America (C. a. occidentalis), Eurasia (C. a. alexandrinus) from southeastern England, southern Sweden and into Russia, south to north Africa, the Red Sea region, Saudi Arabia, Somaliland, northwestern India, Ceylon (C. a. seebohmi), southeastern China and Japan (C. a. dealbatus) and Java (C. a. javanicus) (Fig. 2.2). Although Clancey (1975) gives the most southerly locality of a migrant C. alexandrinus as Zaire, a recent record from Namibia has been confirmed (R.K. Brooke pers. comm.). The less polytypic C. marginatus is found in Africa south of the Sahara (Fig. 2.2). Charadrius marginatus marginatus is found along the

FIGURE 2.2

Global distribution of the superspecies Charadrius alexandrinus.
C. alexandrinus (▨), C. marginatus (⊗) and C. ruficapillus
(▣). Al = C. a. alexandrinus, De = C. a. dealbatus, Ni = C. a.
nivosus, Te = C. a. tenuirostris, Oc = C. a. occidentalis, Se =
C. a. seebohmi, Ja = c. a. javanicus, Ma = C. m. marginatus, Me =
C. m. mechowii, Po = C. m. pons, Ten = C. m. tenellus, Ar = C. m.
arenaceus

southwestern coast of southern Africa, from the Cape Peninsula northwards to Angola (Fig. 2.3). The range of C. m. arenaceus extends along the southern and eastern Cape coasts into Mozambique (Fig. 2.3), and that of C. m. tenellus is restricted to the island of Madagascar (Fig. 2.2). Along the coast and inland river banks of Mozambique and Botswana northwards into West Africa and Liberia C. m. mechowi is found. C. m. pons is the subspecies which occurs along the coast of Somalia, and Kenya (Fig. 2.2).

Populations of Kentish Plovers (C. a. alexandrinus) in Sweden, Norway, Holland and Great Britain, have declined greatly (Bannerman 1960) and the Snowy Plover (C. a. nivosus) is considered a threatened population in North America (Johnsgard 1981). Unfortunately densities are only available for the coastal populations of the southern African subspecies of C. marginatus i.e. C. m. marginatus and C. m. arenaceus (Fig. 2.3). The greatest densities are reached by C. m. marginatus along the Namibian and western Cape coasts, reaching maximum densities of 7 birds km⁻¹ (Hockey et al. 1983) or 8 birds km⁻¹ (Chapter 1) in the southwestern Cape. The densities of C. m. arenaceus decrease markedly from the southwestern Cape, along the eastern Cape and into Natal where they occur at densities of <1 bird km⁻¹. Although there is little information available as to just how 'resident' the populations of White-fronted Sandplovers in southern Africa are, there were four pairs of birds in a southwestern Cape study area, which were apparently resident throughout a 12-month study (Chapter 1). There are records of similar site tenacity over many years for this species in Natal (W.J. Lawson, SAOS Nest Record Cards). White-fronted Sandplovers which are found along river banks in Zambia and Zimbabwe are

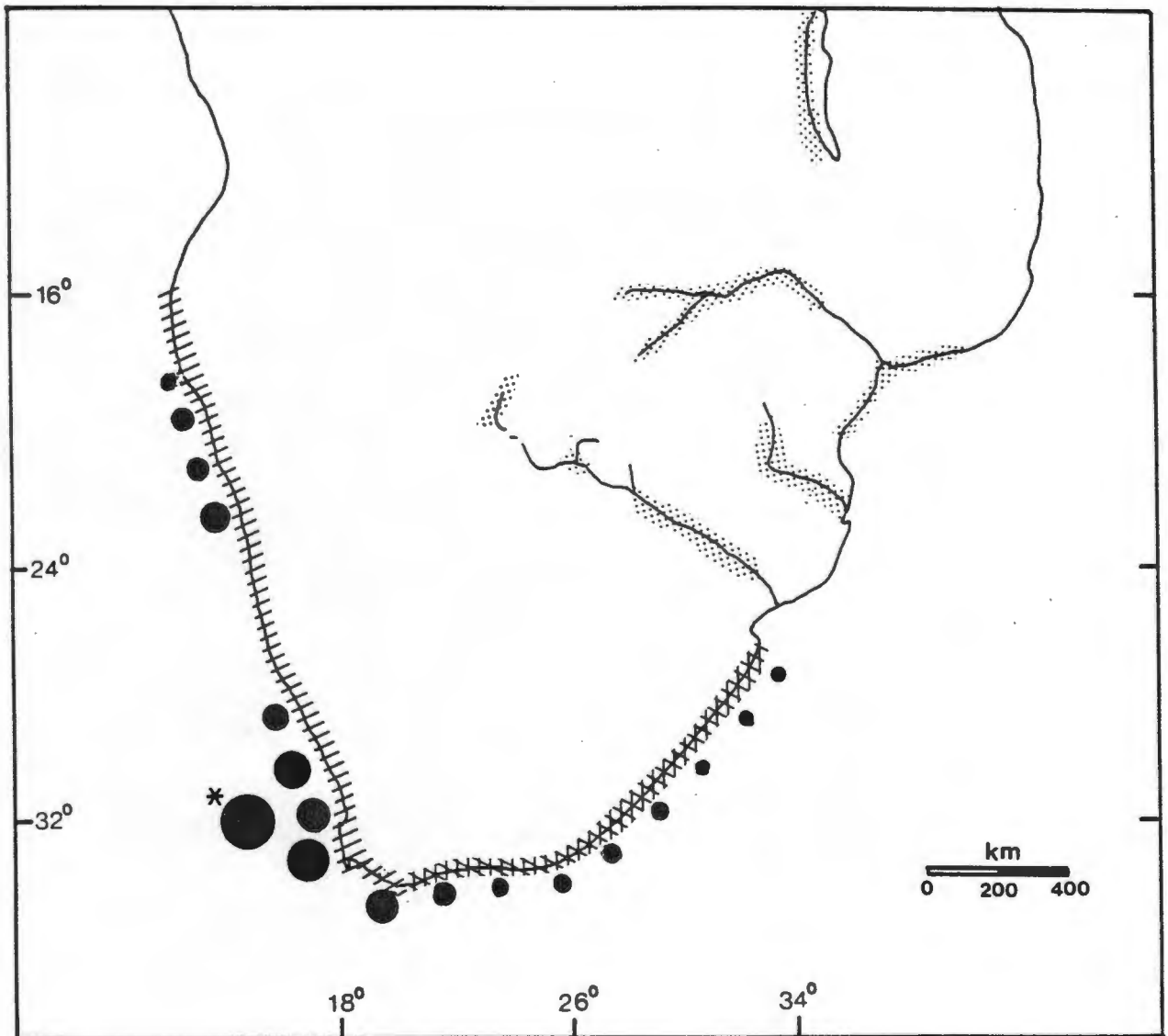


FIGURE 2.3

Southern African distribution of Charadrius marginatus after Clancey (1977). C. m. marginatus (▨), C. m. arenaceus (⊠) and C. m. mechowi (⊞). Densities are given where information are available. ● = 2 birds km⁻¹, ● = 6 birds km⁻¹, ● = 8 birds km⁻¹, * larger density from Chapter 1

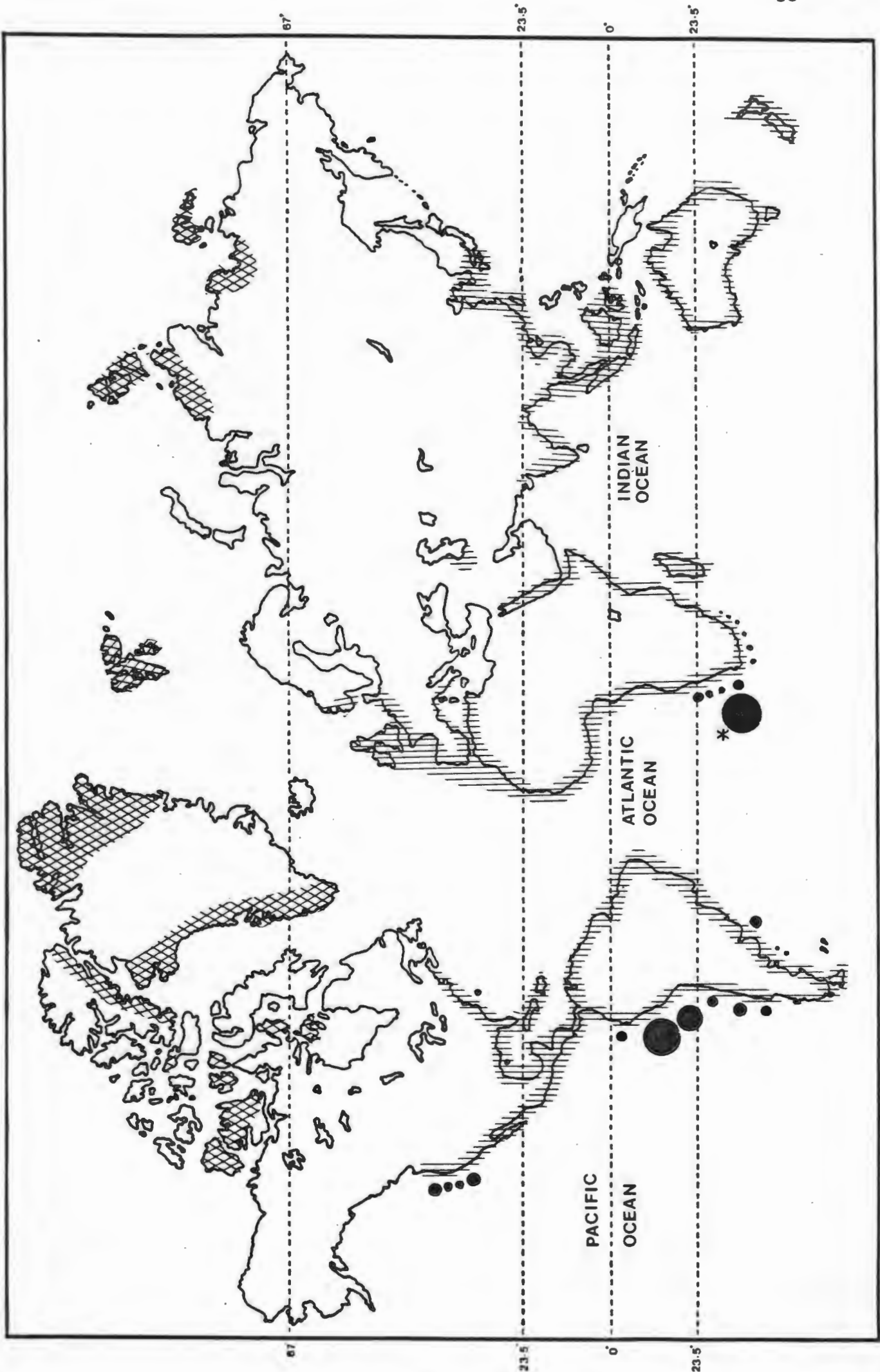
known to undertake local migrations to the coast, prior to the onset of the rainy season, to avoid the danger of flooding (Benson et al. 1971).

Sanderlings generally winter along tropical and temperate sandy beaches south of about 45° N (Fig. 2.4). They can be found along the coasts of all the continents in varying densities (Myers et al. 1985). The Sanderlings' breeding range is limited to the Holarctic regions north of 65° N, along the Canadian arctic islands, Greenland, Alaska, Svalbard, Severnaya Zemlya and New Siberian islands and the Taimyr Peninsula in Russia. Just how these North American/Greenland and Siberian breeding populations distribute themselves over their wintering ranges remains unclear (R.W. Summers et al. in litt.; Myers et al. 1985). Wintering birds which are known to breed in Greenland and Siberia have been observed wintering in southern Africa (Summers 1975; R.W. Summers et al. in litt.).

Boreal mid-winter densities of wintering Sanderlings are greater along the Pacific coasts than the Atlantic coasts of the Western hemisphere (Fig. 2.4). The greatest densities are found along the South American Pacific coasts reaching more than 120 birds km⁻¹. In southern Africa, data from broad-scale atlas accounts indicate densities ranging from 122 birds km⁻¹ along the Namibian coast to about 3 birds km⁻¹ along the Natal coasts (Hockey et al. 1983; Chapter 1; Fig. 2.4). These southern African densities would then be comparable to those along the Californian coast. However, densities during the austral mid-summer, recorded during an intensive survey in the southwestern Cape (Chapter 1; Fig. 2.4), are greater than 180 birds km⁻¹, densities exceeding those recorded by Myers et al. (1985) for the Pacific coast of South America.

FIGURE 2.4

Global distribution of Calidris alba. Breeding distribution (☒), wintering distribution (▨). Densities are given where information are available. ● = 30 birds km⁻¹, ● = 60 birds km⁻¹, ● = 120 birds km⁻¹, * larger density from Chapter 1



Comparison of Figs. 2.2 and 2.4 indicate that, during the austral summer, there is an enormous overlap in the distributions of members of the superspecies C. alexandrinus and Sanderlings along the continental coasts. The most interesting feature of densities of Sanderlings and White-fronted Sandplovers is that they are greatest along those areas adjacent to local coastal water upwelling, i.e. California, Chile and Peru, Namibia and the southwestern Cape coast of South Africa. One might speculate here that similar patterns might be evident in coastal populations of C. alexandrinus and C. ruficapillus if data were available. Since many behavioural interactions in shorebirds, e.g. aggression, are apparently density dependent (Burger et al. 1979), seasonal changes in the densities of these species on a southwestern Cape sandy beach have been considered in Chapter 3, where their comparative foraging behaviour is discussed.

2.3.3 Morphology

MacArthur and Levins (1967) have demonstrated theoretically that there is a limit to both morphological and/or behavioural similarity between competing species which can allow co-existence - "limiting similarity". Schoener's (1965) theory of "character difference" predicts that size differences in the trophic appendages of co-existing species should be evident. He demonstrates that differences in bill size reflect differences in the nature of their food. In southern Africa, Sanderlings are significantly heavier, have longer and narrower bills, longer wings, thicker legs and longer middle toes than White-fronted Sandplovers (Table 2.1). The longer wings of Sanderlings are presumably an adaptation to facilitate their migrations. Sanderlings with their longer, narrower bills can potentially

TABLE 2.1

A SUMMARY OF WHITE-FRONTED SANDPLOVER AND SANDERLING MENSURAL VARIABLES

Variable	White-fronted Sandplover		Sanderling		Inter-species differences	
	males	females	males	females		
Mass (g)	\bar{X}	48.37	50.17	55.47	58.87	$\underline{P} < 0.001$ ^b
	S.D.	3.64	4.43	4.94	4.67	
	n	15	22	15	23	
			ab		ab	
		NS		$\underline{P} < 0.01$		
Bill length (mm)		21.91	22.01	30.41	31.69	$\underline{P} < 0.001$
		1.01	1.43	1.36	1.47	
		83	91	28	61	
			NS		$\underline{P} < 0.001$	
Bill width (mm)		4.45	4.42	3.47	3.45	$\underline{P} < 0.001$
		0.60	0.40	0.70	0.65	
		69	68	13	39	
			NS		NS	
Wing length (mm)		110.45	111.93	120.86	122.75	$\underline{P} < 0.001$
		14.35	18.71	4.07	3.87	
		83	91	28	61	
			NS		$\underline{P} < 0.05$	
Leg length (mm)		26.82	26.33	26.03	26.41	NS
		1.41	1.62	1.63	1.36	
		83	91	28	61	
			NS		NS	
Leg width (mm)		1.45	1.53	1.75	1.68	$\underline{P} < 0.001$
		0.27	0.40	0.42	0.40	
		82	90	28	61	
			NS		NS	
Middle toe length (mm)		1.69	1.62	1.83	1.83	$\underline{P} < 0.001$
		0.43	0.11	0.54	0.50	
		79	80	19	52	
			NS		NS	

^a inter-sexual differences within each species

^b NS = no significant difference

extract food from greater depths within the substratum, than can White-fronted Sandplovers whose shorter, stouter bills are better adapted to pecking food from the surface of the substratum (Burton 1974). Indeed, the Sanderling/White-fronted Sandplover bill length ratio of approximately 1.4 is high. This is consistent with Schoener's (1965) idea that differences in the dimensional and physical properties of their food or their environment should enable these species to partition their habitats or microhabitats. In the southwestern Cape, Sanderlings do in fact forage predominantly below the surface of the substratum, and White-fronted Sandplovers are mainly surface feeders (Chapter 3).

The determination of the sex of individual shorebirds is desirable, since there are documented sexual differences in behaviour (e.g. Zwarts 1980; Puttick 1981; Goss-Custard et al. 1982), which may play an important role(s) in the segregation of wintering populations. I speculate here that Sanderlings which undergo the long migration to southern Africa are socially less successful birds, maybe younger less experienced birds, or sex-linked subordinate birds. Longer migrations by this species might not only be a function of decrease in avian predation or food availability, as has been suggested by Myers et al. (1985) for western hemisphere populations, but also a trade-off between both these variables and experience. Perhaps that is why, in southern Africa, birds from both major breeding areas are found. To test this hypothesis for southern African populations of Sanderlings, one would need to first understand the distribution of sexes amongst the wintering populations. If my hypothesis is correct we should see a latitudinal segregation of the sexes. A latitudinal segregation of sexes for North American populations of Sanderlings has been refuted (Myers 1981).

Statistically univariate t-tests show no inter-sexual morphological differences amongst White-fronted Sandpipers, but in Sanderlings females are heavier, have longer bills and wings than do males. As expected, discriminant functions analysis also showed no discriminating variables between White-fronted Sandplover sexes. Only bill length entered the discriminating equation in Sanderlings. Bill length allowed 75% of the known-sex males to be successfully classified, and 70.5% of the females, as compared with the more than 90% successful classifications of Californian Sanderlings using this technique (Maron & Myers 1985). Technically, this means that by knowing the bill length of southern African Sanderlings we should be able to sex them 'reasonably' well. In southern Africa, sexing Sanderlings on bill length alone is difficult since it would appear that birds breeding in both Greenland and Siberia winter here, and that these populations are mainly recognisable by differences in bill length (Summers 1975; R.W. Summers et al. in litt.). Thus, inter-sexual differences in this species, could be confused with differences which result from different breeding origins. Since the southern African population appears to be heterogenous in breeding origins, discriminant functions analysis will not distinguish between sexes accurately. We should perhaps use laparotomy (Maron & Myers 1985) as a more effective means of successfully determining the sexes.

2.4 Summary

The Kentish or Snowy Plover (Charadrius alexandrinus), the Red-capped Plover (C. ruficapillus) and White-fronted Sandplover (C. marginatus) have a wide global distribution. Although, considered by some systematists to be conspecific, they are considered here

to retain their specific status, as allospecies of a superspecies C. alexandrinus. White-fronted Sandplovers are found in Africa from approximately 15° N along the marine coasts and, to a lesser extent, along the banks of larger rivers. Although there is little information available as to the degree of site tenacity in many of these African populations, the population at Ouskip was apparently 'resident' throughout a 12-month period of intensive study. Densities of White-fronted Sandplovers and Sanderlings were greatest along those shores adjacent to areas of local upwelling in the coastal waters. Sanderlings breed during the boreal summer in the Arctic and tundra regions of the northern hemisphere, north of 65° N latitude. During the boreal winter/austral summer, they migrate to continental coasts and islands, between 60° N and 60° S latitudes, in varying densities.

Mensural comparisons between White-fronted Sandplovers and Sanderlings indicate that Sanderlings are sexually dimorphic, and that White-fronted Sandplovers are not. In Sanderlings, females are heavier, have longer bills and longer wings than males. Discriminant functions analysis was not successful in separating the sexes, due to the fact that southern African populations of this species, are from different breeding populations, which are morphologically distinct, by differences in bill length. Although White-fronted Sandplovers and Sanderlings are similar in size, in comparison with the other avian species regularly inhabiting sandy shores, Sanderlings are heavier and have longer bills, wings and legs than White-fronted Sandplovers, and as such can potentially exhibit different foraging tactics.

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CHAPTER 3

COMPARATIVE FORAGING BEHAVIOUR OF WHITE-FRONTED
SANDPLOVERS AND SANDERLINGS ON A SOUTH AFRICAN SANDY BEACH

3.1 Introduction

In South Africa, Sanderlings Calidris alba and White-fronted Sandplovers Charadrius marginatus are more abundant on sandy than on rocky shores (Summers et al. 1977). Together they account for about 90% of the abundance of shorebirds on southern African sandy shores (Siegfried 1981) which are geologically and biologically unstable biotopes. Sandy shores also exhibit great spatio-temporal variation in the biomass of invertebrates (Brown 1964; Bally 1981) which form the bulk of the prey of many shorebird species (Rheeder 1951; Burton 1974).

The Sanderling, a Holarctic migrant, has a polyandrous mating system and is territorial on its breeding grounds (Parmelee 1970; Parmelee & Payne 1973; Pienkowski & Green 1976). However, it exhibits both territorial and non-territorial behaviour on its wintering grounds (Burger et al. 1979; Pitelka et al. 1980; Myers & Myers 1979; Silliman et al. 1977; Duffy et al. 1981). It is a non-territorial, flock-feeding species in its southern African wintering grounds (Maclean 1985). The White-fronted Sandplover, by contrast, is a resident, monogamous, territorial species with relatively solitary feeding habits in southern Africa (Summers & Hockey 1980).

Since Sanderlings and White-fronted Sandplovers use the same dynamic sandy shore biotope in the southwestern Cape, I sought to identify and explain differences between their foraging behaviour in the light of current competition theory (Cody 1974;

Wiens 1983), especially since there appears to be overlap in their diets (Appendix 1). More particularly, my aims were to compare foraging methods and the spatio-temporal use of a sandy beach by Sanderlings and White-fronted Sandplovers, focusing on six questions:

1. Are the foraging patterns exhibited by White-fronted Sandplovers and Sanderlings a function of tidal cycle and/or time of day?
2. Do White-fronted Sandplovers and Sanderlings forage equally in different microhabitats?
3. Is there seasonal variation in the spatio-temporal foraging patterns exhibited by these two species?
4. Do White-fronted Sandplovers and Sanderlings use different foraging methods?
5. Do these species exhibit intra- and/or inter-specific aggression?
6. Do densities of White-fronted Sandplover and Sanderling vary seasonally?

3.2 Methods

3.2.1 Study areas and observation methods

This study was carried out between January 1977 and February 1978, along a 1.5-km stretch of exposed sandy beach bounded at one end by rocky outcrops at Ouskip (33° 44'S 18° 46'E), 25 km north of Cape Town (Fig. 3.1). In order to establish whether the foraging activities of Sanderlings and White-fronted Sandplovers were influenced by tidal cycle, time of day or a combination of both, I observed individuals of both species and flocks of Sanderlings from dawn to dusk during six days in January 1977 (i.e. near the mid-point of their stay in South

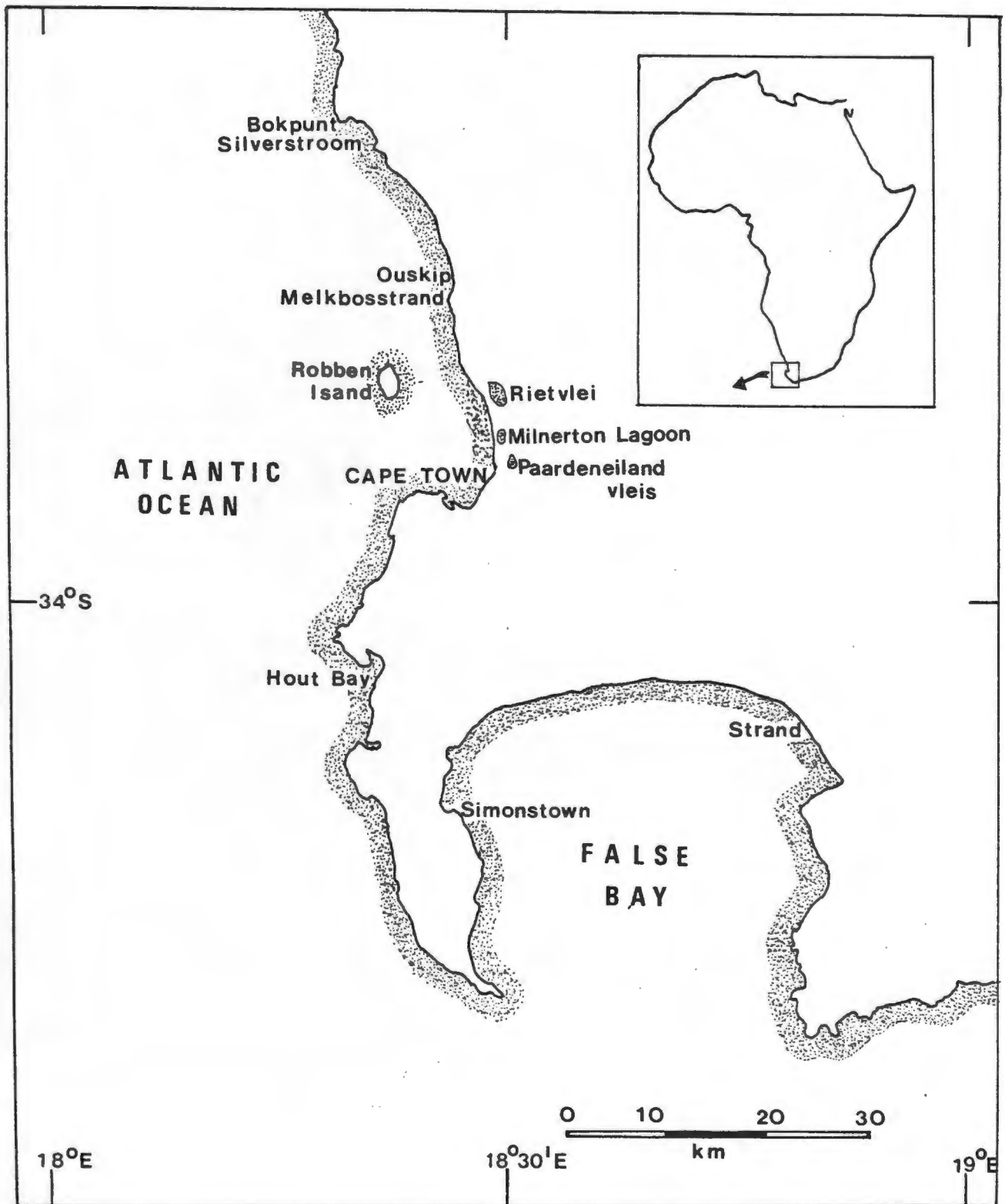


FIGURE 3.1

The southwestern Cape Province, South Africa, showing the location of the Ouskip study area

Africa). These six days included both spring and neap tides, with low tides and high tides at different times of the day. The foraging behaviour of both species was recorded at 15 min intervals along the length of the beach, using the instantaneous scan method (Altmann 1974). Care was taken not to record each bird more than once during each scan. For security reasons, this study was limited to the period between dawn and dusk. On the basis of the patterns observed during this bout of observations, I decided that each unit of daily observational time should include at least one high tide and one low tide.

From February 1977 to January 1978 a minimum of 30 hours per month (120 instantaneous scans) was spent recording: the foraging behaviour of the birds present in the study area; their foraging microhabitat; the method by which they captured their prey; and, in the case of Sanderlings, flock size. Intra-specific and inter-specific aggressive encounters were recorded ad libitum (Altmann 1974).

Six foraging microhabitats (hereafter zones) were recognized: water's edge (A); the wet area approximately 0.3 m from the water's edge (B); the wet area covered by a film of water (C); the damp sand with no water film (D); the drift line including the bulk of the kelp cast ashore (E); and dry sand (F). In order to identify potential variation in the availability of recognized microhabitats throughout a tidal cycle, the area of each zone exposed in the study area in summer was measured at hourly intervals between high and low water springs.

The five modes of foraging method recognized were: taking an organism from the surface of the substratum (pecking); inserting the bill into the substratum for less than half its length

(jabbing); inserting the bill into the substratum for more than half its length (probing); a rapid probing motion during which the bill is quickly removed during each successive probe (stitching, sensu Burton 1974); and a similar rapid movement, except that the bill is not removed between each successive probe (ploughing). Jabbing and probing were difficult to distinguish in the White-fronted Sandplover, because of its short bill. For this reason, and for comparative purposes, these two modes were combined. Ploughing and stitching were observed only in Sanderlings and were lumped as one category.

In order to learn more about the prey taken by these two shorebirds, and to test for inter-specific competition between White-fronted Sandpipers and Sanderlings, 45 White-fronted Sandpipers and 75 Sanderlings were shot at Silverstream (33° 34'S, 18° 19'E) about 15km north of Ouskip (Fig. 3.1). If one species were being excluded from a particular habitat by the other, removal of the dominant species should lead to an increase in niche breadth of the subordinate species.

In order to determine possible alternative foraging sites for Sanderlings ad hoc counts were made along the Paardeneiland vleis, Milnerton Lagoon and Rietvlei (Fig. 3.1) as I travelled to Ouskip.

3.2.2 Statistical methods

Cluster analysis (Field & McFarlane 1968; Anderberg 1973) and multidimensional scaling (Kruskal 1964) were used to compare samples (monthly data for each species) according to their attributes (foraging mode and zone). In these analyses, the Bray-Curtis similarity measure (Bray & Curtis 1957) was used,

and, in cluster analyses, a group-average sorting method (Lance & Williams 1967) was used to create dendrograms. These two multivariate techniques are complementary (Field *et al.* 1982). Cluster analysis is useful in identifying hierarchical structure (i.e. groups and sub-groups of samples), whereas multidimensional scaling is better at illustrating multivariate trends or gradients. The information statistic test (Field 1969) was used to identify habitat and foraging behavioural variables which characterize the groups obtained by cluster analysis and multidimensional scaling. In order to avoid problems due to fluctuating sample sizes, monthly sample values were based on proportions of the total number of birds of each species observed each month. The austral seasons referred to below are: spring = September - November, summer = December - February, autumn = March - May, and winter = June - August. Number of hours of daylight, wave height, rainfall data and ambient temperature (Maxwell & Rattey 1977-1978; Weather Bureau 1977-1978; Anon. 1977-1978a; Anon. 1977-1978b) were extracted for the period of study and compared with behavioural observations to determine their potential influence on the birds' foraging. All statistical tests used are described in Sokal & Rohlf (1981), unless specified otherwise in the text.

3.3 Results

3.3.1 Temporal and spatial variation in habitat use

During January 1977, both White-fronted Sandpipers and Sanderlings foraged unevenly throughout the day ($\chi^2 = 23,19$, $df = 11$, $P < 0.025$; $\chi^2 = 184,31$, $df = 11$, $P < 0.005$), but their foraging appeared to follow a tidal cycle rather than a diurnal cycle (Fig. 3.2). At both spring and neap tides, Sanderlings

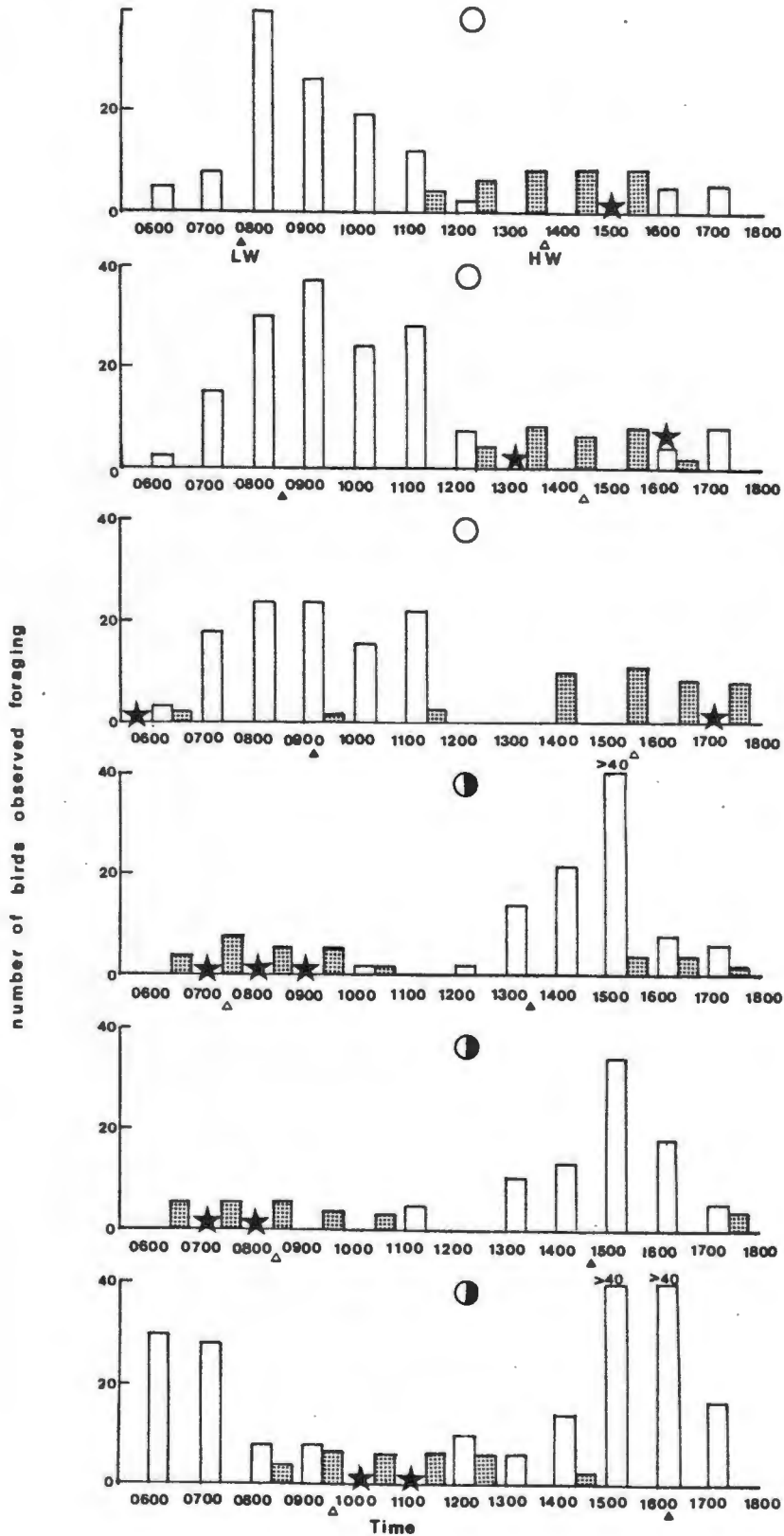


FIGURE 3.2

Numbers of foraging Sanderlings (□) and White-fronted Sandpipers (▤) as a function of time of day. Data were collected on two sets of three consecutive days; first set over spring tides (○), and second set over neap tides (◐). Roosting Sanderlings (★). LW = low tide; HW = high tide

foraged mainly before and immediately after low tides ($\chi^2 = 661.61$, $df = 5$, $\underline{p} < 0.005$; Fig. 3.2), when the mean amount of intertidal area exposed (i.e. zones A to E) was higher than that exposed during the period preceding and following high tide (Fig. 3.3). White-fronted Sandplovers concentrated their foraging around mid to high tide ($\chi^2 = 198.47$, $df = 5$, $\underline{p} < 0.005$; Fig. 3.2), when the mean amount of exposed intertidal area was significantly less ($\underline{t} = 7.75$, $df = 34$, $\underline{p} < 0.001$; Fig. 3.3). These patterns continued throughout the period of study ($\chi^2 = 1966.63$, $\chi^2 = 137.41$, $df = 5$, $\underline{p} < 0.05$; Figs 3.4 & 3.5).

Spatial segregation (Fig. 3.6 & 3.7) shows much the same pattern as temporal segregation in these two species, Sanderlings fed in the wetter microhabitats (i.e. zones A - C in Fig. 3.7; $\chi^2 = 1081.85$, $df = 5$, $\underline{p} < 0.005$), and White-fronted Sandplovers in the drier zones (i.e. zones D - F in Fig. 3.7; $\chi^2 = 101.27$, $df = 5$, $\underline{p} < 0.005$). For both species, the use of microhabitats varied with tidal time (Fig. 3.8). However, the mean spatial (zones utilized) foraging niche breadth (Cody 1974) of Sanderlings was significantly greater than that of White-fronted Sandplovers ($\underline{t} = 4.35$, $df = 19$, $\underline{p} < 0.001$); Table 3.1).

3.3.2 Seasonal patterns in spatial and temporal habitat use

In autumn, spring and early summer, Sanderlings increased their foraging time (Mann-Whitney U-test, $\underline{U} = 25$, $\underline{p} < 0.001$; Fig. 3.4), whereas White-fronted Sandplovers fed significantly more during the winter months ($\underline{U} = 58$, $\underline{p} < 0.001$; Fig. 3.4). During the winter, there were fewer daylight hours, lower ambient temperatures, and less exposed intertidal area due to significantly greater mean wave height (F. Shillington pers. comm.; $\underline{t} = 7.41$, $df = 314$, $\underline{p} < 0.001$; Fig. 3.9). Moreover, the

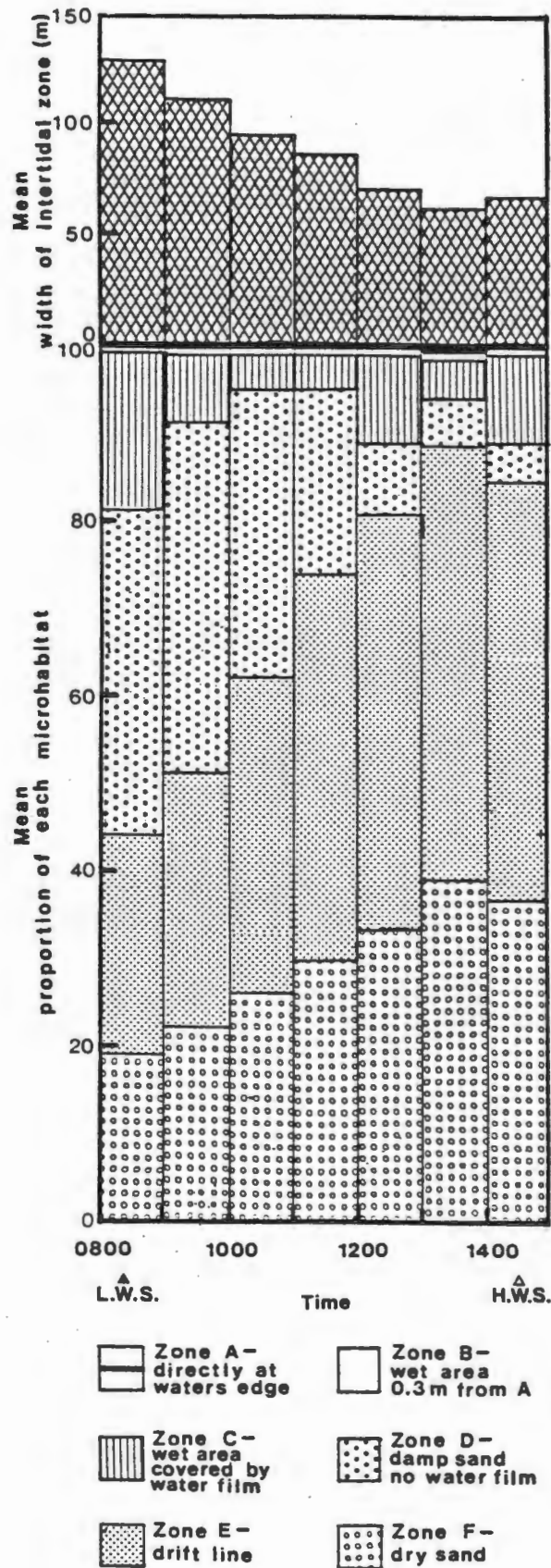


FIGURE 3.3

Variation in the amount of intertidal area and the relative proportion of six microhabitats at various stages of a spring tide

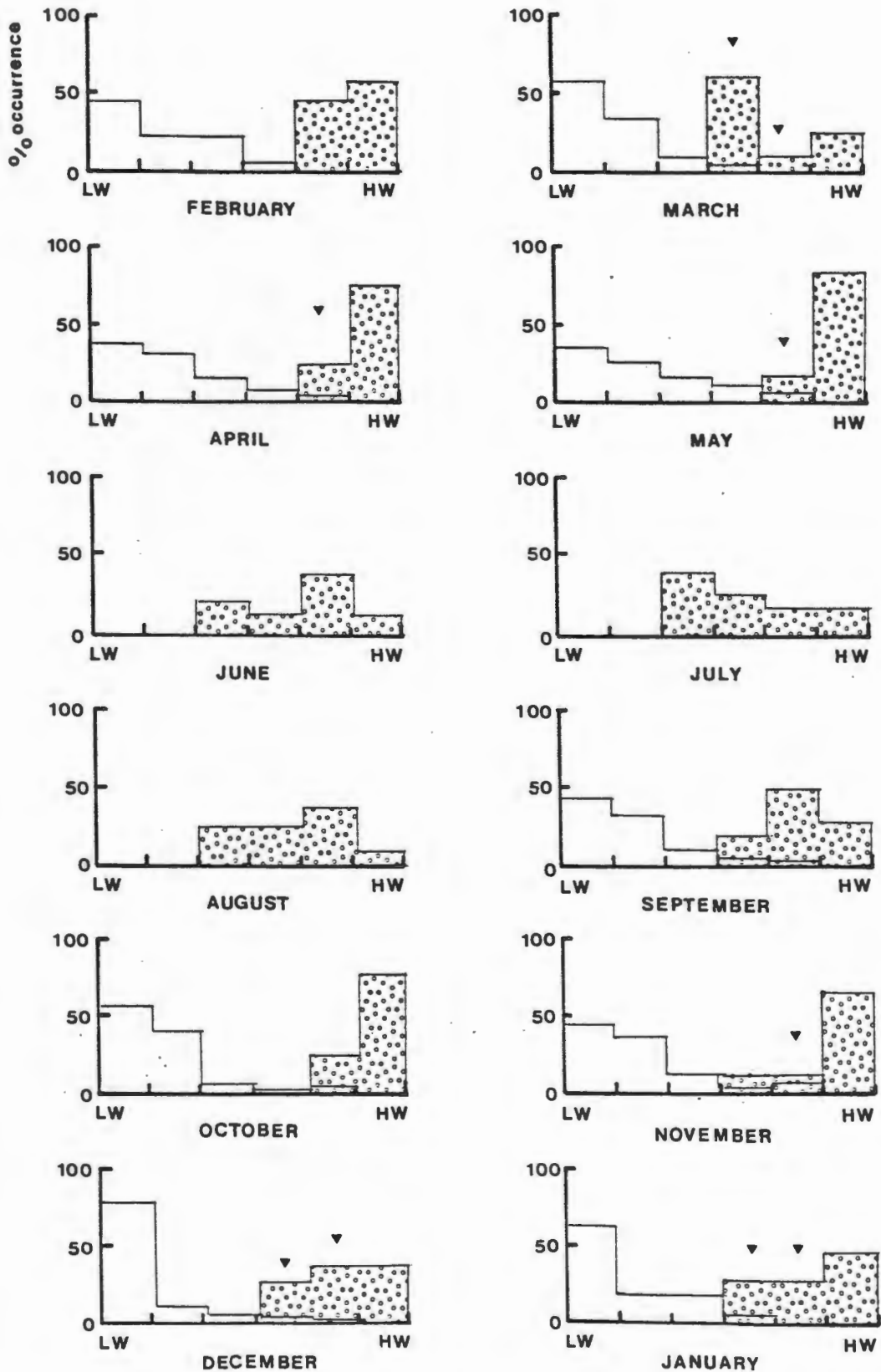


FIGURE 3.4

Foraging activity of Sanderlings (\square) and White-fronted Sandplovers (\square) as a function of tidal time for 12 consecutive months February 1977 to January 1978. Inter-specific aggressive encounters (\blacktriangledown). LW = low tide; HW = high tide

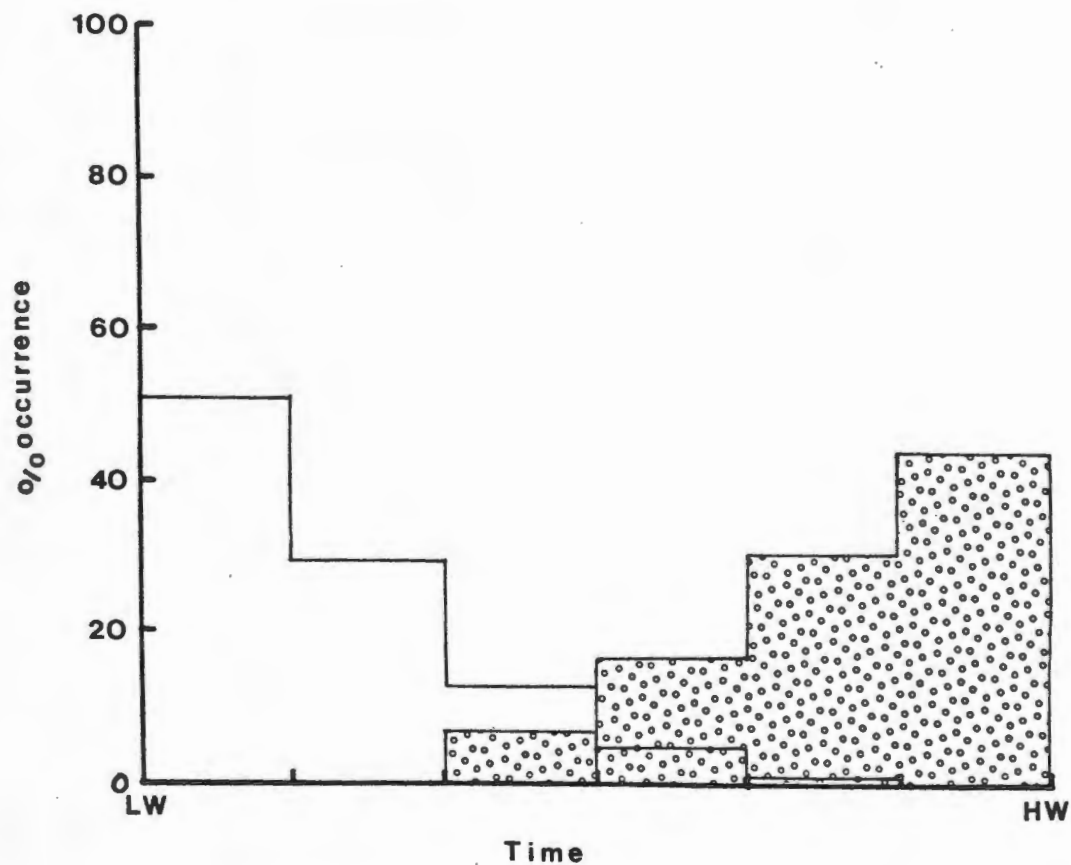


FIGURE 3.5

A summary of foraging activity of Sanderlings (\square) and White-fronted Sandplovers (\square) as a function of tidal time. Data for February 1977 to January 1978 are combined. Inter-specific aggressive encounters (\blacktriangledown). LW = low tide; HW = high tide.

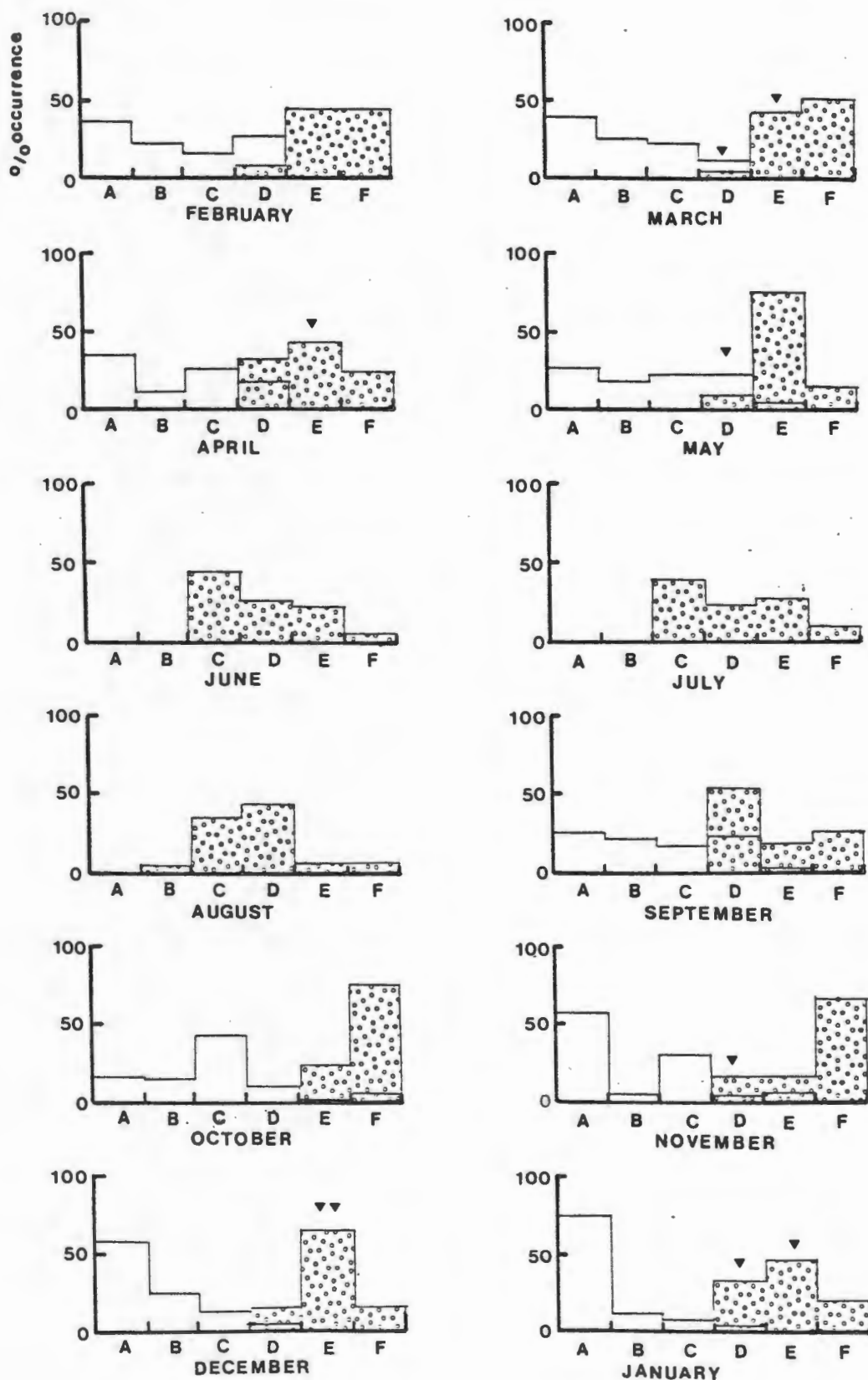


FIGURE 3.6

Foraging activity of Sanderlings (□) and White-fronted Sandplovers (▨) as a function of microhabitat, for 12 consecutive months. Inter-specific aggressive encounters (▼). A is zone at water's edge and F dry sand

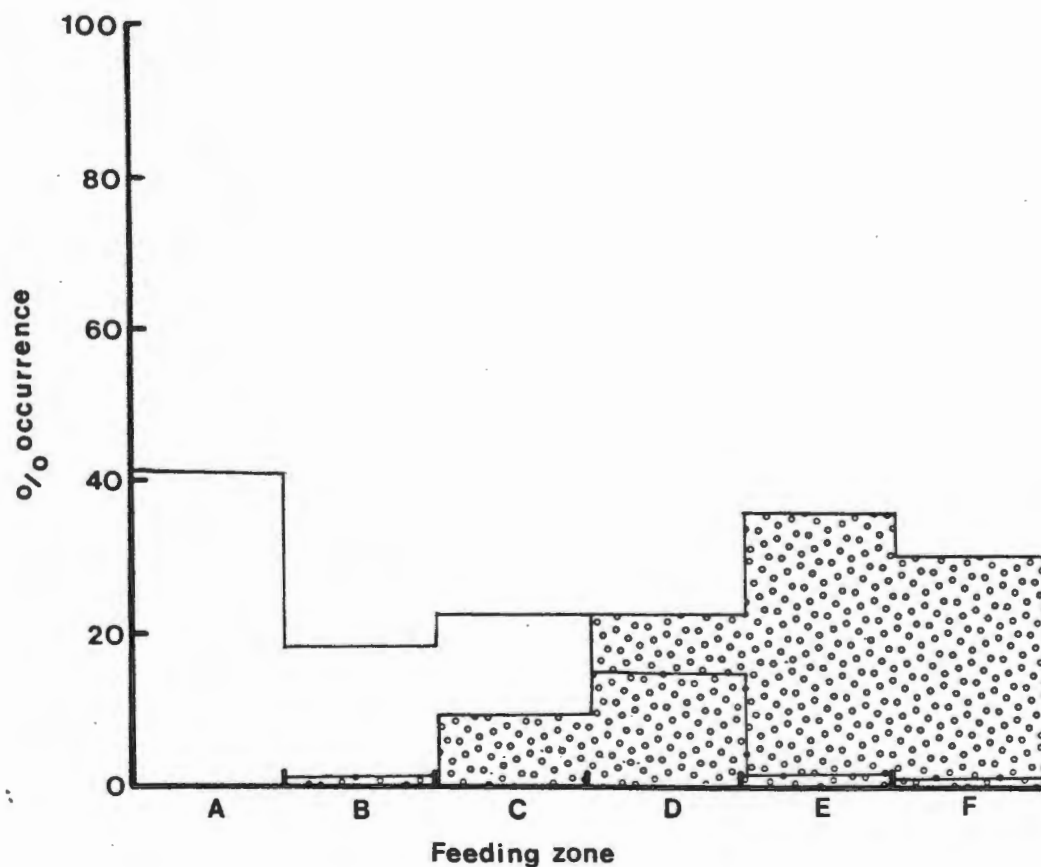


FIGURE 3.7

A summary of foraging activity of Sanderlings (\square) and White-fronted Sandplovers (\square) as a function microhabitat. Data for February 1977 to January 1978 are combined. Inter-specific aggressive encounters (\blacktriangledown). A is zone at water's edge and F dry sand.

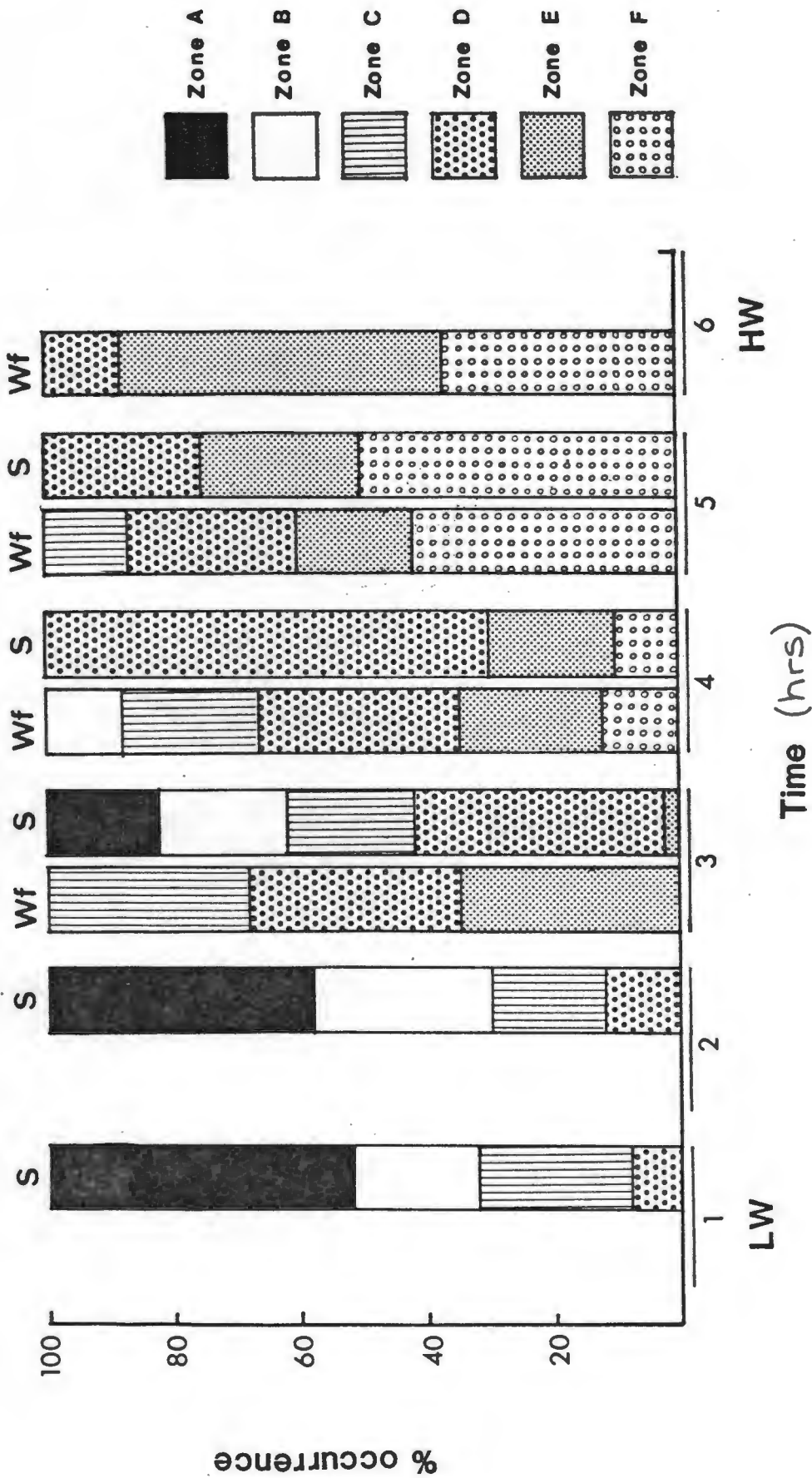


FIGURE 3.8

Variation in use of microhabitat by White-fronted Sandplovers and Sanderlings in relation to tidal time

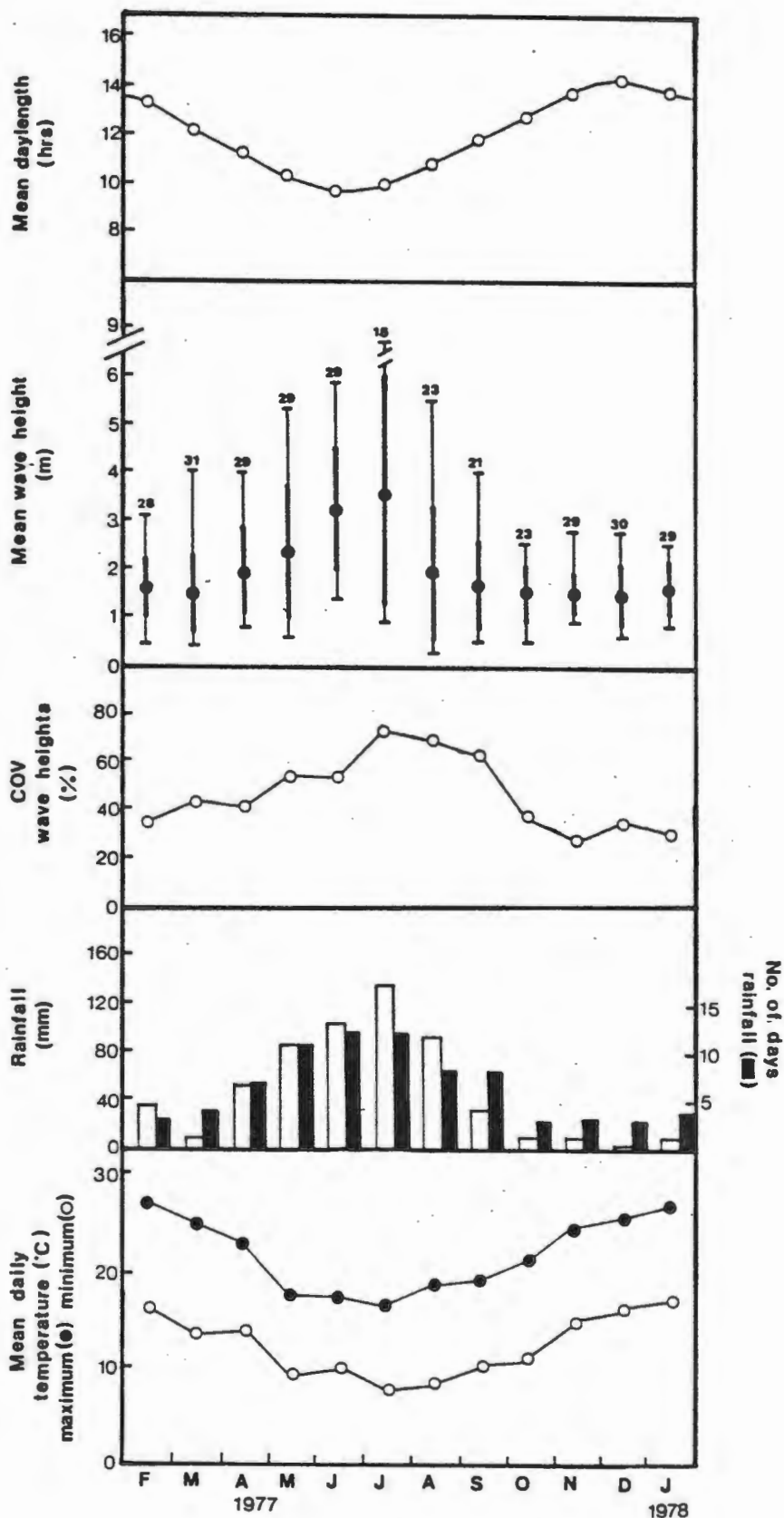


FIGURE 3.9

Variation in mean hours of daylight, mean wave height, coefficient of variation of wave height (standard deviation (—), range (—) and sample size), total rainfall, number of days of rainfall and mean minimum and maximum temperature at Ouskip for the period February 1977 - January 1978

amount of exposed intertidal area was probably also less predictable due to the higher relative variability (coefficient of variation = COV) of mean wave heights during winter ($\bar{X} = 57.33$, $SD = 9.29$, $t = 3.43$, $df = 10$, $p < 0.01$; Fig. 3.9). In spring, White-fronted Sandplovers supplemented intertidal foraging by feeding in freshwater ponds in nearby sand dunes, which were the result of winter rains (Fig. 3.9). Sanderlings were never observed foraging in these ponds. However, there is preliminary evidence that they switch habitats (see below). By the end of November, all ponds in the study area used by White-fronted Sandplovers had dried up. During spring tides, Sanderlings roosted on neighbouring rocky outcrops. However, at neap tides, Sanderlings roosted on the same rocks and on the sand above high water neaps level. White-fronted Sandplovers remained on their territories virtually continuously.

The mean temporal (tidal time) foraging niche breadth (Cody 1974) of Sanderlings was also significantly greater than that of White-fronted Sandplovers ($t = 5.73$, $df = 19$, $p < 0.001$; Table 3.1). Niche overlap between the two species (in terms of tidal time) increased significantly in May and September [i.e. immediately prior to the Sanderlings' departure from and immediately after their return to the study area ($t = 3.89$, $df = 7$, $p < 0.001$; Table 3.1)]. The mean foraging niche breadth (zones utilized) (Fig. 3.4) for White-fronted Sandplovers was greater in winter than during the rest of the year ($U = 55$, $p < 0.0001$). The increase in diversity of tidal hours utilized during winter indicates that, not only were White-fronted Sandplovers spending more time feeding, but they also distributed the time spent in each microhabitat more evenly (Table 3.2).

For Sanderlings, the foraging niche breadths were greatest

TABLE 3.2
 DIVERSITY OF EIGHT FORAGING VARIABLES AND OVERALL FORAGING DIVERSITY OF WHITE-FRONTED SANDPLOVERS (WF) AND SANDERLINGS (S) AT OUSKIP

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	
Tidal Hr. usage	Wf	0.639	0.955	0.562	0.473	1.292	1.340	0.321	1.044	0.562	0.868	1.090	1.067
	S	1.206	0.937	1.289	1.435	*	*	*	1.261	0.975	0.166	0.777	1.030
Zone Usage A-F	Wf	0.897	1.077	0.760	1.210	1.210	1.308	0.223	1.010	0.562	0.868	0.908	1.036
	S	1.353	1.329	1.406	1.475	*	*	*	1.435	1.459	0.043	1.143	0.819
Foraging Methods Zone A	Wf	-	-	-	-	-	-	-	-	-	-	-	-
	S	0.994	0.760	1.042	0.942	*	*	*	0.729	0.416	0.810	0.565	0.591
Foraging Methods Zone B	Wf	-	-	-	-	-	-	-	-	-	-	-	-
	S	0.891	0.807	0.856	0.859	*	*	0.000	0.838	0.673	0.777	1.061	0.917
Foraging Methods Zone C	Wf	-	-	-	-	-	-	-	-	-	-	-	-
	S	0.748	0.860	0.537	0.514	0.000	0.500	0.451	0.595	0.423	0.403	0.802	0.848
Foraging Methods Zone D	Wf	0.000	0.000	0.562	0.000	0.500	0.637	0.562	0.693	-	0.000	0.000	0.562
	S	0.340	0.184	0.162	0.165	*	*	*	0.256	0.246	0.000	0.000	0.000
Foraging Methods Zone E	Wf	0.673	0.451	0.673	0.662	0.693	0.683	0.000	0.637	0.637	0.693	0.599	0.500
	S	-	-	0.562	0.500	*	*	*	0.000	0.000	0.000	-	-
Foraging Methods Zone F	Wf	0.377	0.000	0.000	0.000	0.000	0.000	0.501	0.537	0.402	0.377	0.693	0.000
	S	-	-	-	-	*	*	*	-	0.000	-	-	-
Total foraging diversity	Wf	1.870	1.944	1.867	1.740	2.160	2.212	2.155	2.001	1.671	1.906	1.989	2.008
	S	2.243	2.143	2.329	2.406	*	*	*	2.358	2.271	2.187	2.055	2.006

^a $H = \frac{1}{\sum P_i \log P_i}$ where P_i is the importance value for each species (foraging variable) (Shannon and Weaver 1963).

- = species was not observed foraging in this zone.

* = Sanderlings not in study area

Wf = White-fronted Sandplovers

S = Sanderlings

during the pre- and post-migratory phases ($U = 159$, $P < 0.001$). Mean foraging niche breadth for each species did not differ significantly when tidal time or foraging zones utilized are considered independently as resources ($\underline{t} = 1.17$, $df = 22$; $t = 0.001$, $df = 16$, Table 3.1). In other words, both the spatial and temporal measures of niche overlap are equally good. Neither measures of niche overlap increased during the Sanderlings' pre- and post-migratory phases ($\underline{t} = 1.37$, $df = 7$, $P > 0.50$; Table 3.1), indicating that Sanderlings did not increase the scope of their foraging area, but rather the amount of time spent foraging in their preferred microhabitats during these periods. Moreover, during these phases, the temporal diversity of foraging tended to be higher than for the rest of their stay, indicating a more equal use of available foraging time. There was no marked increase in the diversity of foraging zones utilized by Sanderlings during this same period.

3.3.3 Foraging methods

The method of foraging used in each of the different microhabitats appeared to be similar for both species (Fig. 3.10). In the wetter microhabitats (zones A and B), Sanderlings employed stitching and ploughing more often than jabbing and probing, which they used more often than pecking (Fig. 3.10). When White-fronted Sandpipers were recorded in zone B the method they used for prey capture was jabbing and probing. In the drier upper regions, both species captured prey by means of pecking. Sanderlings never employed stitching and ploughing in the drier microhabitats above zone C (Fig. 3.10), and there was no appreciable seasonal variation in the foraging methods employed by each species in each zone (Fig. 3.11). During winter, when

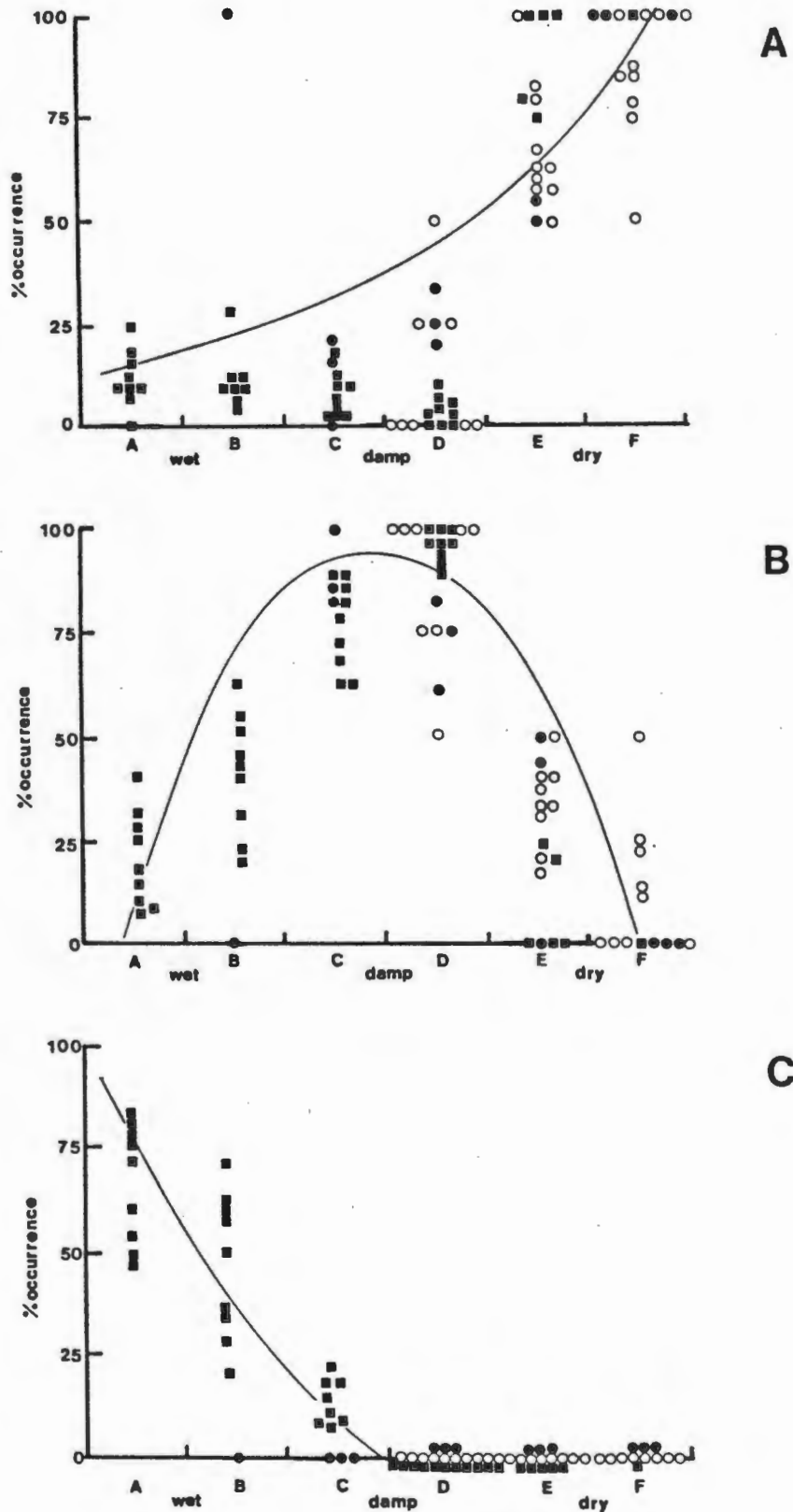
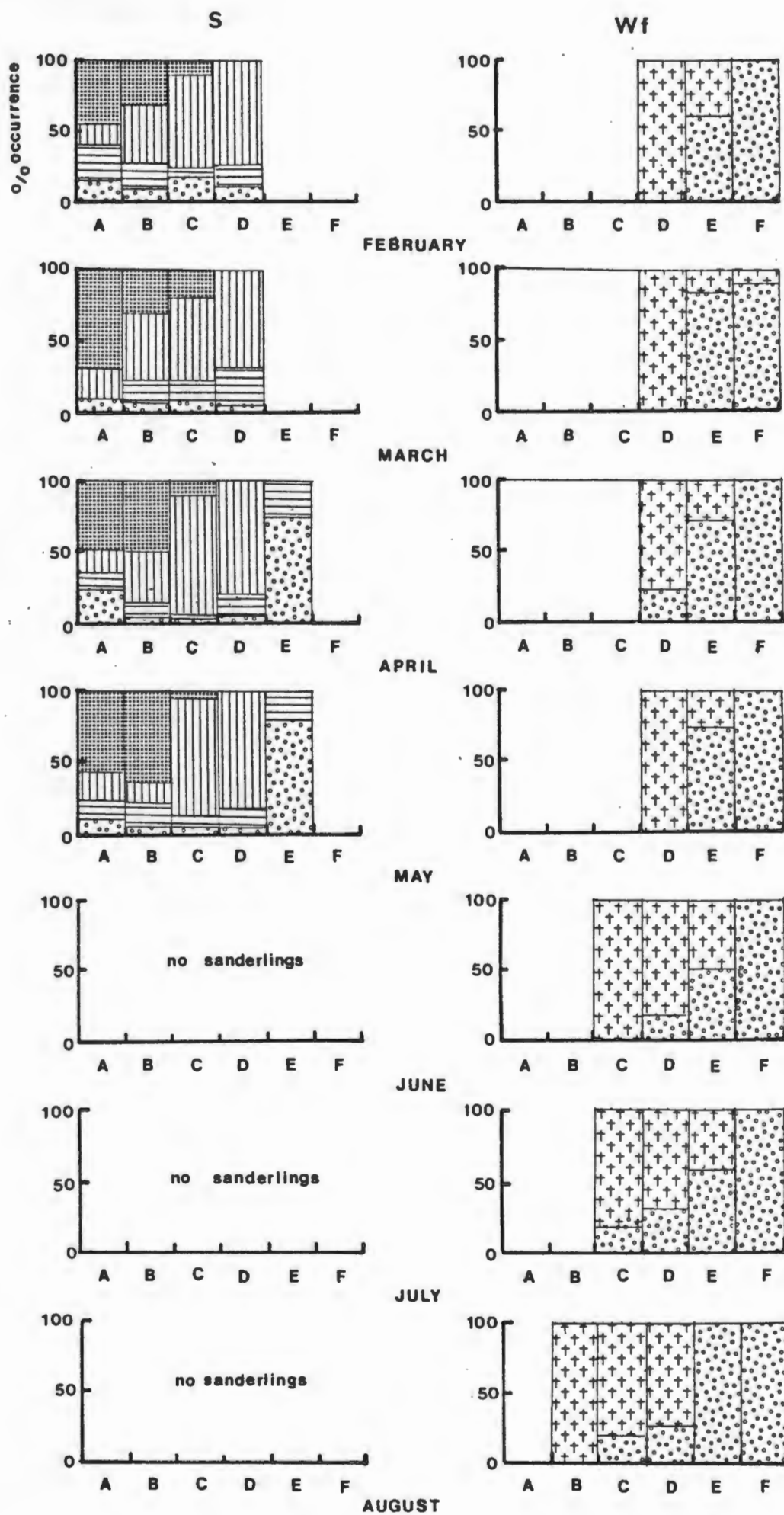


FIGURE 3.10

Variation in foraging methods of Sanderlings and White-fronted Sandplovers in six microhabitats. Solid lines indicate trends. All Sanderlings (■); White-fronted Sandplovers when Sanderlings present (○); White-fronted Sandplovers winter (●). (A) Pecking; (B) Jabbing and probing; (C) Ploughing and stitching



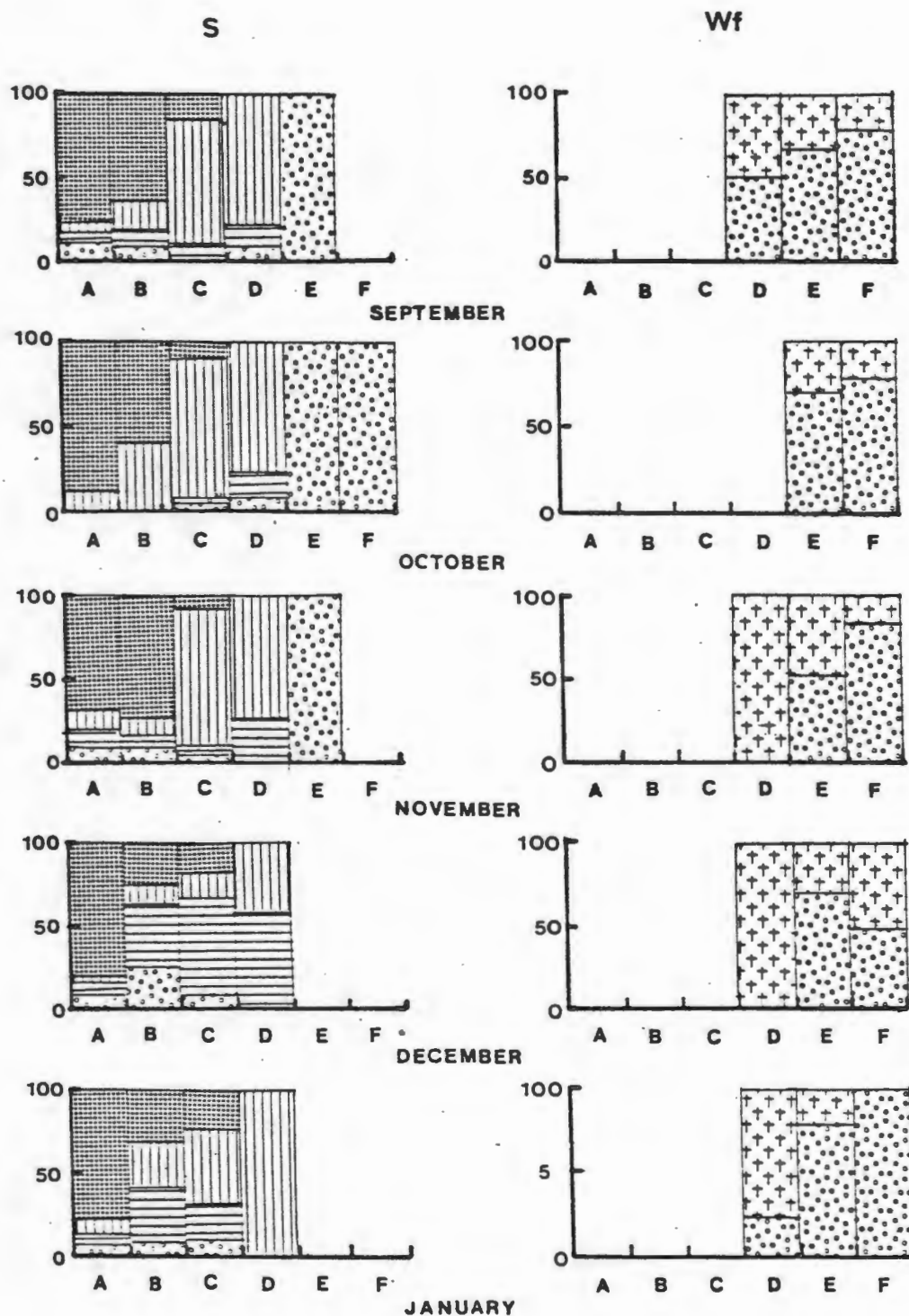


FIGURE 3.11

Variation in foraging methods of Sanderlings and White-fronted Sandplovers as a function of microhabitat during 12 consecutive months. Ploughing and stitching (▣); jabbing (▤); probing (▥); jabbing and probing (⊕) and pecking (◼)

White-fronted Sandplovers extended their range of foraging zones, their pecking activity in zones C and D increased (Fig. 3.11). The mean diversity of foraging methods between the two species differed significantly ($t = 9.44$, $df = 19$, $P < 0.001$), and was significantly greater for Sanderlings in the pre- and post-migratory phases than during the remainder of the study period ($t = 4.67$, $df = 7$, $P < 0.001$). However, foraging method diversity did not differ significantly for White-fronted Sandplovers between the austral winter and the remainder of the year ($t = 0.54$, $df = 10$, $P > 0.30$).

3.3.4 Multivariate analyses of foraging activities

The results of the cluster and multidimensional scaling analyses (Figs 3.12 & 3.13, Groups Wf and S) and information statistic tests (Table 3.3) reveal marked spatial and temporal differences in the foraging behaviour of these two shorebirds. The White-fronted Sandplover cluster (Wf) subdivides into two smaller sub-clusters (1 and 2). Sub-cluster 1 consists of those months during which Sanderlings were present. Sub-cluster 2 consists of the three months of winter during which Sanderlings were absent from the study area. The Sanderling cluster also divides into two sub-clusters (3 and 4). Sub-cluster 4 consists of the pre- and post-migratory periods for Sanderlings, and sub-cluster 3 of the remaining months during which they were present in the study area. The Sanderling cluster (S) has significantly higher values for foraging in the wetter microhabitats (zones A - C), whereas the White-fronted Sandplover cluster (Wf) has higher values for foraging in the drier zones (zones D - F). Temporally, the Sanderling cluster is distinguished by higher foraging activity in the first three tidal hours (i.e. around low tide), whereas the White-fronted Sandplover cluster has higher

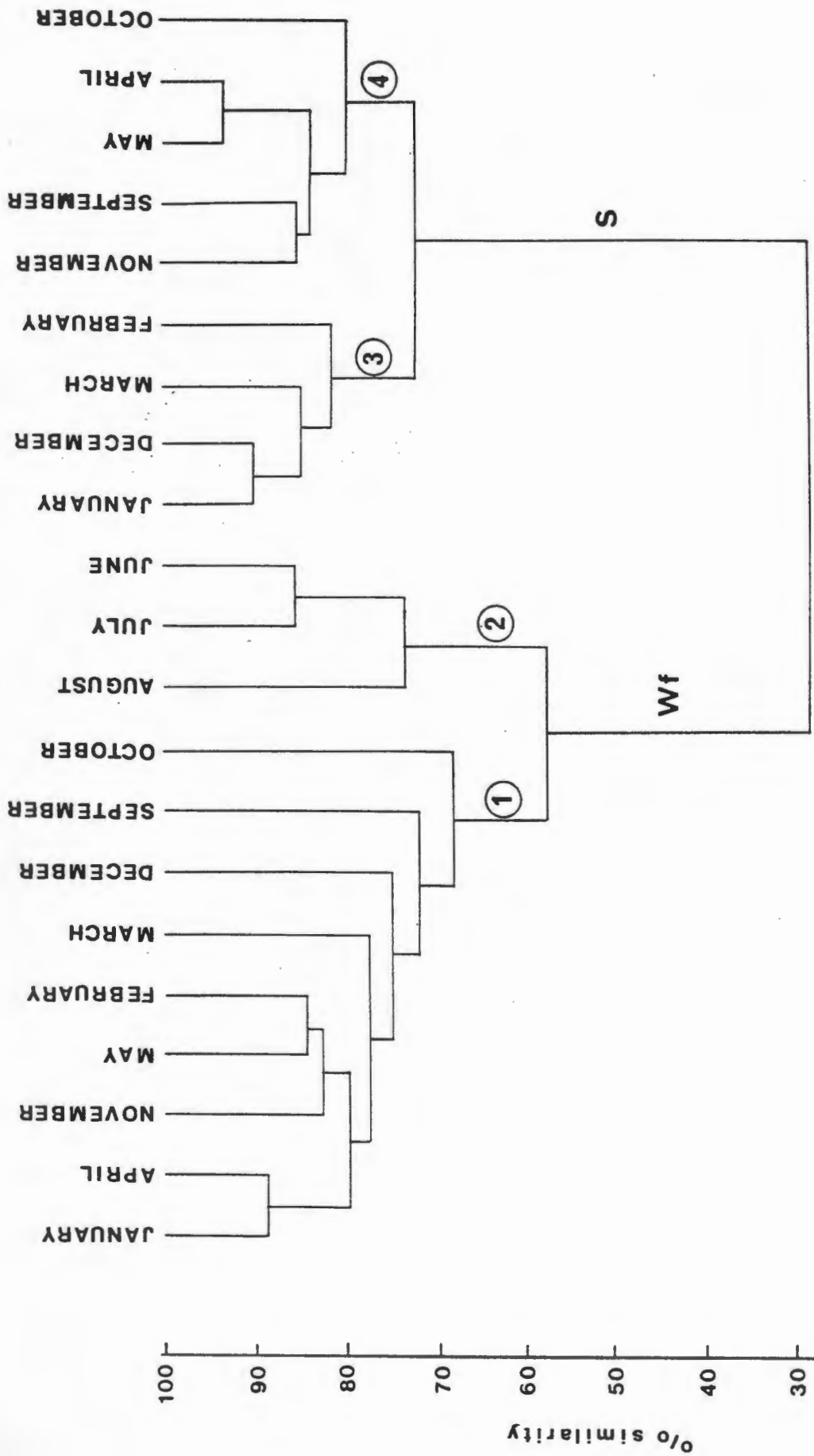


FIGURE 3.12

The results of a cluster analysis of White-fronted Sandplover and Sanderling foraging activity according to 15 foraging variables listed in Table 3.3. Sub-cluster 1 = Spring, Summer and Autumn; White-fronted Sandplover; sub-cluster 2 = Winter; White-fronted Sandplover; sub-cluster 3 = Summer; Sanderlings; sub-cluster 4 = Pre- and post-migratory phases: Sanderlings

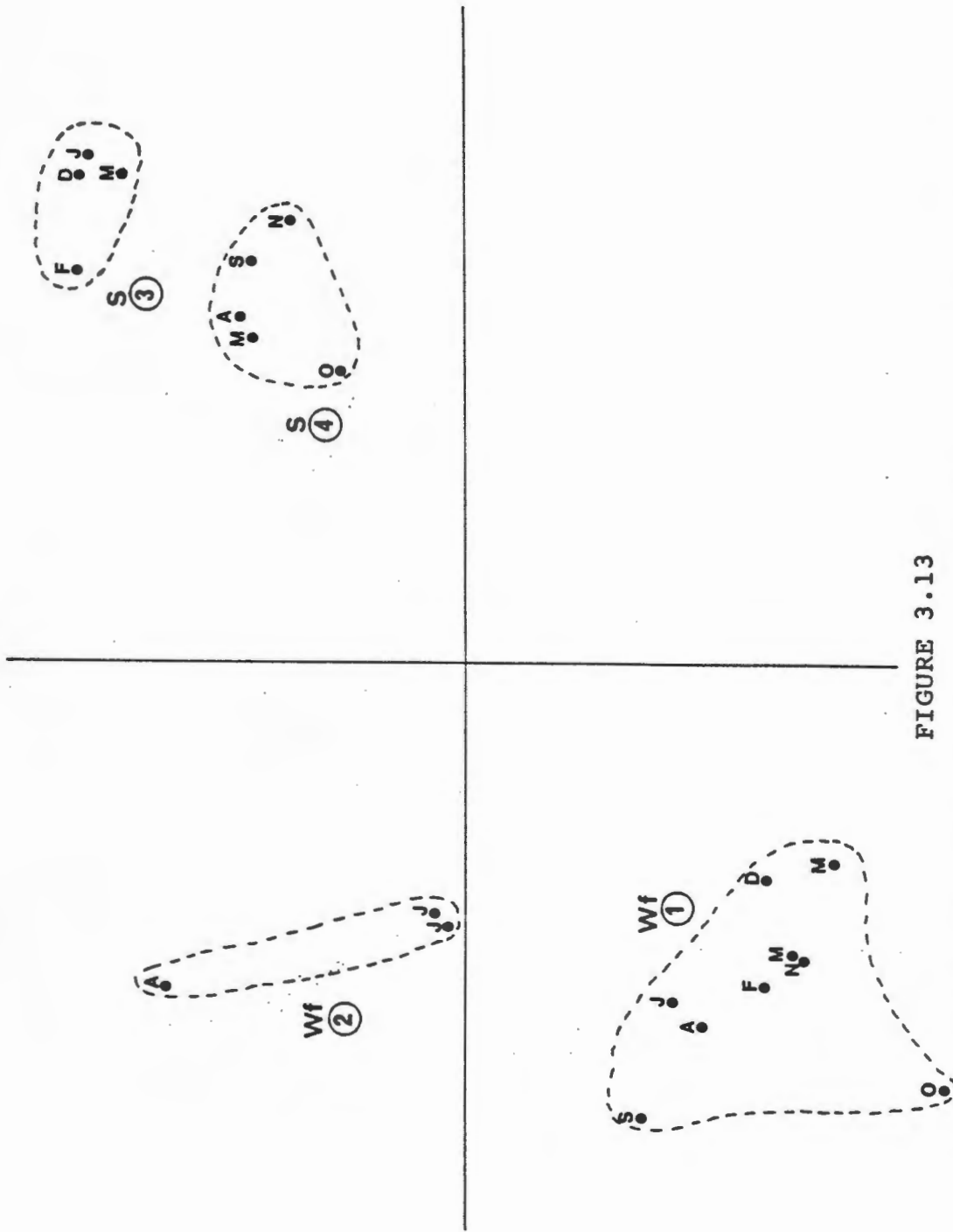


FIGURE 3.13

Ordination of White-fronted Sandplover and Sanderling foraging activity according to the similarity matrix generated in Fig. 3.12. Sub-cluster 1 = Spring, Summer and Autumn; White-fronted Sandplovers; sub-cluster 2 = Winter; White-fronted Sandplovers; sub-cluster 3 = Summer; Sanderlings; sub-cluster 4 = Pre- and post-migratory phases: Sanderlings

TABLE 3.3

RESULTS OF INFORMATION STATISTIC TESTS, COMPARING SANDERLING AND WHITE-FRONTED SANDPLOVER FORAGING ACTIVITY ACCORDING TO THE GROUPS AND SUB-GROUPS RECOGNIZED IN FIGS.

3.12 AND 3.13

Variable	All White-fronted Sandplovers (Wf) vs All Sanderlings (S)	White-fronted Sandplovers non winter (1) vs White-fronted Sandplovers winter (2)	Sanderlings non pre- and post-migratory period (3) vs Sanderlings pre- and post-migratory period (4)
First tidal hour (low tide)	** (S) ^{a 1}	NS	(3)2 ** ⁵
Second tidal hour	** (S) ³	NS	** (4) ⁵
Third tidal hour	** (S) ⁷	** (2) ²	NS ⁸
Fourth tidal hour	(Wf) ** ⁶	** (2) ⁵	** (4) ³
Fifth tidal hour	(Wf) ** ⁴	** (2) ⁶	** (4) ³
Sixth tidal hour (high tide)	(Wf) ** ¹	(1) ² **	NS ¹
Zone A (water's edge)	** (S) ²	NS	(3) ¹ **
Zone B	** (S) ⁵	** (2) ³	(3) ⁴ **
Zone C	** (S) ⁶	** (2) ¹	** (4) ²
Zone D	(Wf) ** ⁷	** (2) ⁴	** (4) ⁷
Zone E	(Wf) ** ²	(1) ³ **	** (4) ⁴
Zone F (dry sand)	(Wf) ** ³	(1) ¹ **	** (4) ⁶
Pecking	(Wf) ** ⁵	(1) ⁴ *	** (4) ¹
Jabbing and probing	** (S) ⁸	* (2) ⁷	(3) ³ **
Ploughing and stitching	** (S) ⁴	NS	(3) ⁵ *

* = significant at the 0.05 Level

** = significant at the 0.01 Level

NS = not significant

a = group which is significantly greater

b = importance of variable in discriminating between groups compared (1=most important)

values for the last three tidal hours (i.e. around high tide). The Sanderling cluster is also characterized by higher values for jabbing, probing and stitching; and the White-fronted Sandplover cluster by pecking. These results confirm the univariate analyses discussed above (see Figs 3.2, 3.4, 3.6, 3.11).

The major foraging dichotomy for White-fronted Sandplovers occurred between the winter months (sub-cluster 2) and the rest of the year (sub-cluster 1). White-fronted Sandplovers not only increased their use of the tidal time in winter (Fig. 3.4), but also changed the spatio-temporal distribution of foraging time and space zones, moving into the zones which had been used mainly by Sanderlings. Temporally, they included foraging in the third tidal hour after low tide, increased range into the fourth and fifth tidal hour, and decreased use of the sixth tidal hour. Spatially, in winter, they fed less in the drier zones (zones E & F) and more in the damper zones (zones B - D) (Table 3.3). During spring, summer and autumn they employed pecking significantly more than in winter, during which they jabbed and probed more (Table 3.3).

During their pre- and post-migratory phases (sub-cluster 4), Sanderlings tended to decrease their dependence on the earlier stages of the tide (one hour after low tide) and utilization of the wetter microhabitats (zones A and B), and increase their use of second, fourth and fifth tidal hours and the drier microhabitats (zones C - F). They foraged more by pecking than jabbing and probing during this period (Table 3.3).

3.3.5 Intra- and inter-specific aggression

Intra-specific aggressive encounters were observed throughout

much of the year between neighbouring pairs of territorial sandplovers. These encounters were most intense when a chick was present in one of the territories. Only one incident of intra-specific aggression between Sanderlings was observed, at very high prey densities (Chapter 4). Inter-specific aggressive encounters were short-lived and were always initiated by solitary White-fronted Sandplovers which chased individuals or groups of Sanderlings off their territories. Such incidents were recorded only during those months when there was spatial or temporal overlap in foraging (Figs 3.4 & 3.6). However, when there was temporal overlap these species still tended to forage in different microhabitats (Fig. 3.8), and the spatio-temporal foraging behaviour of Sanderlings at Silverstroom within the area in which White-fronted Sandplovers had been shot did not differ significantly before and after removal of the birds ($\chi^2 = 3.2$, $df = 5$, $P > 0.05$).

3.3.6 Variation in density

The White-fronted Sandplover population at Ouskip remained constant (4 pairs), except in December when two chicks were present in the area, and in January when flocks of juvenile birds wandered intermittently into the area. The abundance of Sanderlings at Ouskip varied considerably from day to day, but was greatest immediately prior to their northward migration from the southwestern Cape (April and May), and lowest in September and October when they returned to Ouskip (Fig. 3.14).

Data collected from ad hoc counts made along the Paardeneiland vleis, Milnerton Lagoon and Rietvlei en route to the Ouskip study area indicate that, when Sanderling numbers were low on arrival at Ouskip, they were high at these three sites (Fig. 3.15).

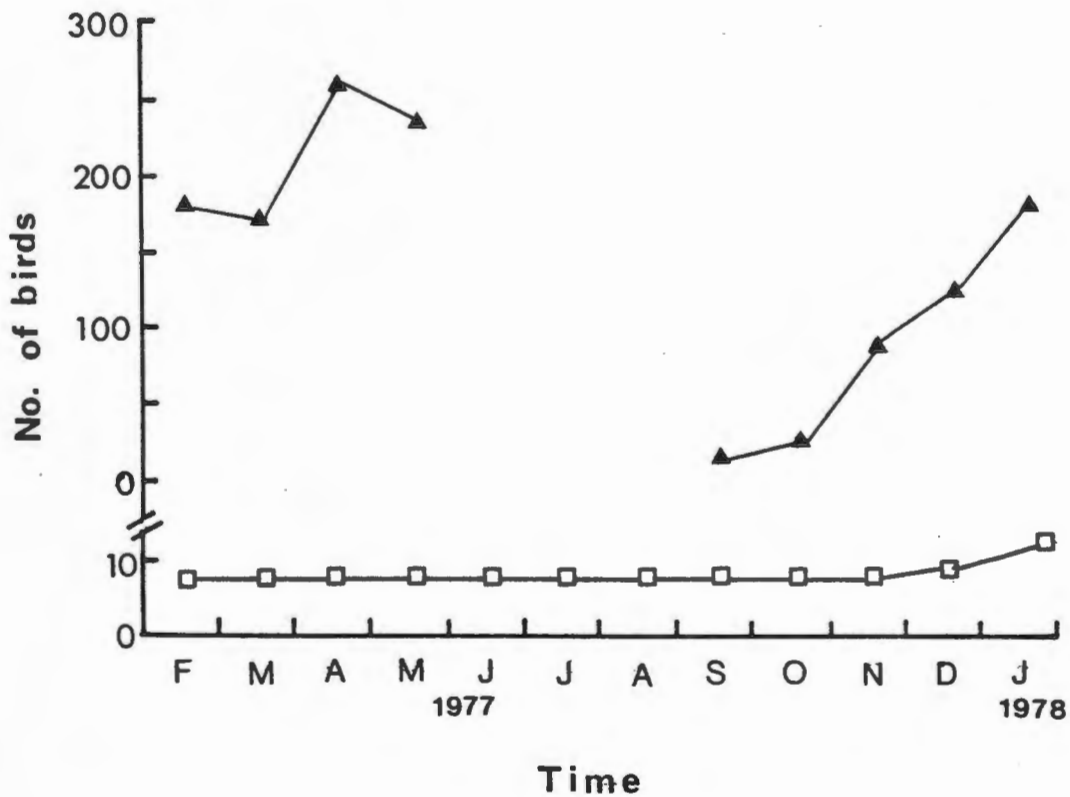


FIGURE 3.14

Mean total number of White-fronted Sandplovers (□) and Sanderlings (▲) at Ouskip, February 1977 to January 1978

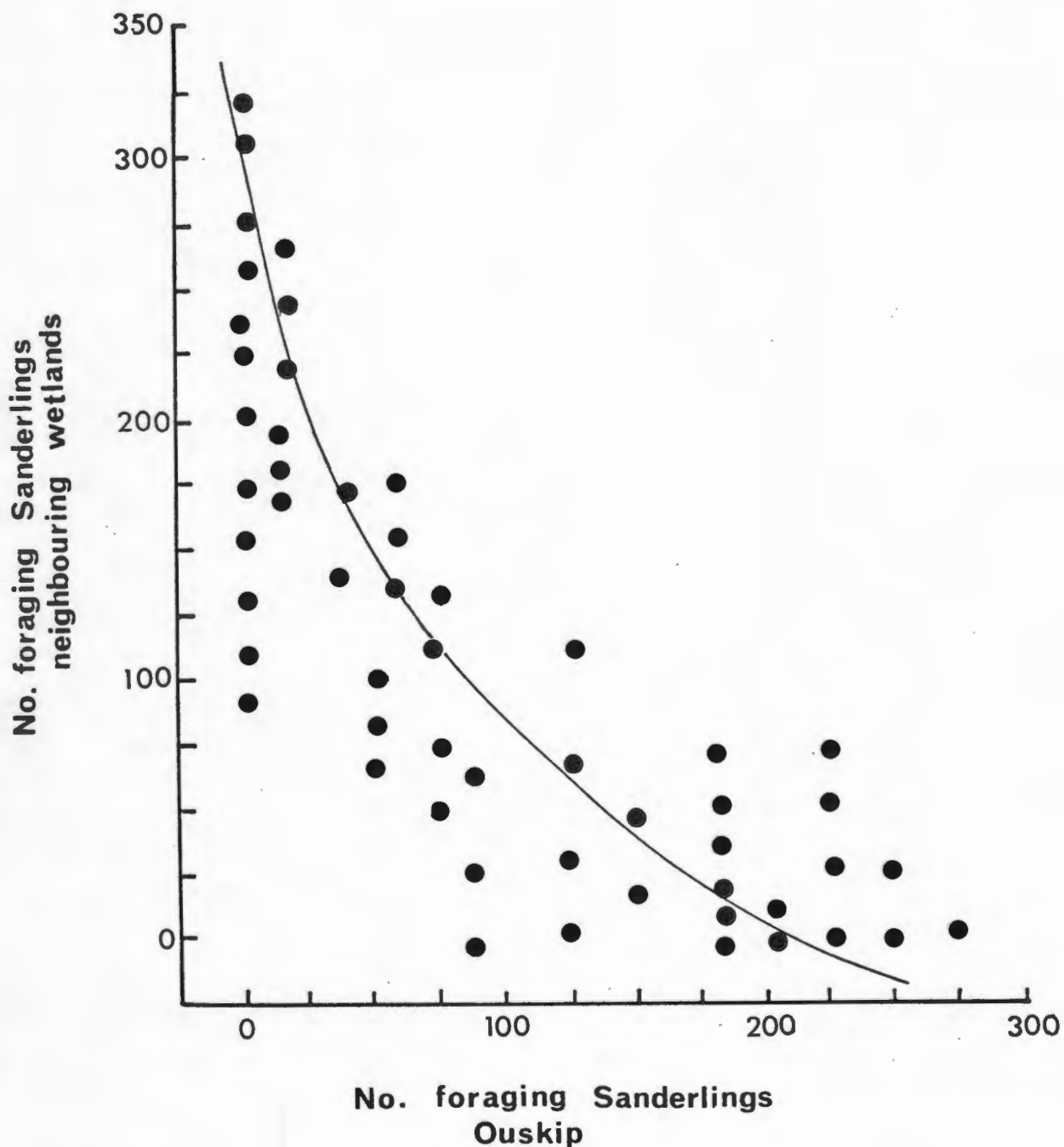


FIGURE 3.15

Numbers of Sanderlings observed foraging on the sandy intertidal at Ouskip, and on nearby wetland habitats. Counts at each habitat were made within 30 minutes of each other. Solid line drawn by eye

3.4 Discussion

3.4.1 Spatio-temporal patterns of habitat use

As predicted by classical competition theory (Hutchinson 1959; Cody 1974; Wiens 1983), White-fronted Sandpipers and Sanderlings appear to partition the Ouskip sandy beach spatially and temporally. Throughout the year, White-fronted Sandpipers tended to feed during higher tides, and in the drier microhabitats. Sanderlings fed mainly at low tide and in the wetter microhabitats. This tidal pattern is presumably due to the effects of prevailing lunar conditions on the pattern of exposure of the intertidal habitat. The next obvious question is: has a tidal cycle in the foraging activities of these two species been documented by previous workers, and, if so, are the trends the same?

Ehlert (1964) recorded a peak in densities of foraging Sanderlings along the North Sea coast immediately after high tide. In Britain, Evans (1980) also found that Sanderlings exhibited a tidal cycle in foraging activities, feeding at low tide and roosting at high tide. Burger et al. (1977), on the east coast of North America, found that, although the concentrations of all shorebirds in the intertidal area were highest following low tide, the number of foraging Sanderlings peaked after both low and high tides. At Bodega Bay, California, Sanderlings fed mainly at mid-high tide on the open beach (Pitelka et al. 1980). McLachlan et al. (1980) found that, on southern Cape beaches, Sanderlings foraged during the early morning and the late afternoon, irrespective of the state of the tide. What then causes Sanderlings from different areas to feed at different stages of the tidal cycle?

One possibility is that, in southern Africa, Sanderlings are prevented from feeding during the later stages of the tidal cycle by territorial White-fronted Sandplovers. This hypothesis might be correct for southern Cape Sanderlings. In this area, White-fronted Sandplovers do not appear to exhibit a tidal foraging cycle (Kapp 1982) and the portion of the tidal cycle around high tide is unoccupied, and therefore available for use by Sanderlings. However, if White-fronted Sandplovers were preventing Sanderlings from foraging at higher tides or in drier microhabitats, removal of territorial White-fronted Sandplovers at Silverstroom should have allowed Sanderlings to extend their use of the tidal cycle, or increase their use of drier microhabitats. They did neither.

The feeding patterns of the White-fronted Sandplover are not particularly surprising, since plovers generally feed on small surface-dwelling invertebrates at higher tidal levels (Pienkowski 1981). The northern hemisphere Kentish or Snowy Plover Charadrius alexandrinus, considered by some authors to be conspecific with the Afrotropical White-fronted Sandplover (Chapter 2), also feeds mainly on the upper reaches of the beach (Recher 1966; Pienkowski 1981). Feeding during high tide possibly minimizes the energetic costs of territorial defence for White-fronted Sandplovers, since they only need to defend a small area of exposed beach. This same argument might well apply to Sanderlings at Bodega Bay, in California, which exhibited territorial behaviour and fed at high tide.

The one documented exception to this pattern concerns a population of White-fronted Sandplovers observed near Port Elizabeth, South Africa. Members of this population apparently

do not display a tidal foraging cycle (Kapp 1982; but see McLachlan et al. 1980). Kapp's study area was a sandy beach surrounded by large systems of dunes which extend for kilometres inland from the beach. These dunes are rich in invertebrate prey (A. McLachlan pers. comm.). Kapp concluded that, although the birds which she studied spent proportionally less time in the intertidal habitat compared with the dune area, their rate of foraging was greatest in the intertidal zone and, hence, that the intertidal area was a more important source of food. Since White-fronted Sandplovers tend to forage on very small prey items (Appendix 1), successful prey capture is very difficult to detect by human observers, and inferences equating success rate with pecking attempts may not be justified. I suggest that the White-fronted Sandplovers studied by Kapp might well have obtained much of their food from the dune area, and used the intertidal only as a supplementary feeding source. This seems to be a reasonable alternative hypothesis, since Strauch and Abele's (1979) research on the feeding ecology of three wintering plover species in Panama showed that the only species which did not exhibit a tidal foraging pattern was the Collared Plover Charadrius collaris which exploited other habitats in addition to the intertidal area.

In the southwestern Cape, kelp is cast ashore along the higher (zone E) reaches of the shore. Insects and crustaceans abound in and about this kelp (Stenton-Dozey 1983), and form a significant part of White-fronted Sandplover diet in the western Cape (Appendix 1). Moreover, these arthropods are most active at high tide (Muir 1977). In the Port Elizabeth area, kelp is not cast ashore, and these prey might well be replaced by food items less dependent on a tidal cycle. A shift to prey with

activity/availability not following a tidal cycle might lessen the need for White-fronted Sandplovers to forage in the intertidal area and thus obscure any tidal foraging cycle.

Bally's (1983) research at a southwestern Cape sandy beach has shown that the biomass of many of the prey species of White-fronted Sandplovers and Sanderlings is concentrated between the mid- and high-tide zones. However, my unpublished data on the distribution of these prey suggest that these distributions change with changing tidal levels, with certain species (e.g. Eurydice longicornis) 'migrating' up and down the beach. Moreover, there are inherent difficulties in measuring food availability from a "bird's point of view" (Myers et al. 1980). Although some Sanderlings tend to roost at high tide, they do not do this at every high tide. Preliminary data from my counts at inland wetlands suggest that Sanderlings sometimes exploit alternative wetland biotopes. This possible habitat switching may maximize the profitability of different habitats, and is also found for Sanderlings wintering in California (Connors et al. 1981). Thus, it appears that the availability of high quality invertebrate prey is the primary factor which influences the foraging patterns of White-fronted Sandplovers and Sanderlings, and Sanderlings may switch habitats to optimize their foraging.

3.4.2 Seasonal variation in foraging patterns

Increases in the range of the tidal cycle used for foraging by shorebirds are usually attributed to difficulty in obtaining food (Evans 1976; Goss-Custard 1979). Difficulty in obtaining food is said to increase with increasing bird densities (Baker 1973, 1974, 1977; Baker & Baker 1973) and environmental variability (Evans 1976). However, Duffy et al. (1981) found no increase in

foraging times and habitats utilized during the high bird density conditions in intertidal habitats in Peru during the austral summer. Another important factor thought to affect the foraging activity of migratory birds is the need to increase fat deposits prior to migration (Berthold 1975).

I therefore propose three hypotheses, which are independent of bird density and climatic variation concerning the patterns discussed above:

- 1) prior to and immediately after migration, Sanderling flocks may be too small, or group cohesion insufficient, to locate patchy food sources. Therefore, individual Sanderlings need to forage for longer periods to satisfy their daily energy requirements (Evans 1976);
- 2) Sanderlings increase their foraging niche breadth when they need to build up fat stores used during migration;
- 3) expansion of the Sanderling foraging niche is a result of relaxation of territoriality by White-fronted Sandpipers.

The first of these hypotheses is dealt with in Chapter 4. The second hypothesis is supported by the fact that Sanderlings in the southwestern Cape increased their body masses immediately prior to migration (Summers & Waltner 1978), and at Ouskip Sanderlings fed at high densities for increasingly longer periods of the tidal cycle and foraged in a wider range of microhabitat types (Figs 3.4 & 3.6). This extension of temporal and spatial habitat use was also evident immediately on their return from their breeding grounds. Moreover, although the mean body mass of Sanderlings during the month after their return to the southwestern Cape is not the lowest mass recorded during their stay here, their fat stores are lower than during the rest of the period (Summers & Waltner 1978). Dick and Pienkowski (1979)

observed that newly arrived migrating shorebirds in Morocco had low body masses and poor body condition. They also noted intensive feeding by shorebirds essentially immediately on their arrival, and that their feeding rates were much higher than those of the established flocks of the same species.

The third hypothesis is supported by the fact that, during the austral spring, at Ouskip White-fronted Sandplovers supplemented their intertidal feeding by foraging in dune ponds, and *might not* need to defend a large foraging area, thereby allowing newly returning Sanderlings to forage more extensively. However, if this were so, why then were Sanderlings able to forage for extended periods during the pre-migratory periods when White-fronted Sandplovers have no supplementary/alternative food source, and why did the Sanderlings not expand their foraging range when White-fronted Sandplovers were removed at Silverstroom?

No first-year Sanderlings were observed at Ouskip, although some remain in the southwestern Cape throughout the year (Pringle & Cooper 1977). Therefore, no data are available for birds free of migratory stress. However, Puttick (1979) found that Curlew Sandpipers *C. ferruginea*, feeding on intertidal mudflats in the southwestern Cape, extended the amount of tidal time spent foraging prior to migration, and that overwintering birds also spent longer periods foraging, presumably a consequence of having to survive the austral winter. Although Duffy *et al.* (1981) found no evidence for a difference in the amount of time spent foraging between summer and winter, they did detect a change between localities ("major habitat types"), and may well have observed similar increases in the foraging activity of the birds

which they studied if their research had encompassed periods of migratory stress as defined herein.

A critical factor in foraging ecology is the relationship between the total resources and the amount of foraging time (Lack 1968). At Ouskip during winter, daylight foraging hours and intertidal feeding area decrease markedly, and shorebird energy requirements should increase due to a decrease in ambient temperature. During this period, White-fronted Sandplovers increased their usage of microhabitats to include areas used by Sanderlings during summer. In Britain, Feare (1966), Goss-Custard (1969) and Goss-Custard et al. (1977) also noted an increase in the time spent foraging by shorebirds (especially smaller species) during winter.

Thus, both White-fronted Sandplovers and Sanderlings exhibited marked seasonal variation in their spatio-temporal patterns of habitat use, and the results of this study suggest that this variation is a response to different physiological requirements (e.g. migration and breeding) and varying environmental conditions (e.g. daylength and temperature).

3.4.3 Foraging methods

In general, sandplover foraging tactics are stereotyped, whereas those of sandpipers are plastic (Baker & Baker 1973; Baker 1974; Pienkowski 1981, 1983a, 1983b). Although the Sanderlings at Ouskip were essentially 'probe feeders', they have retained the ability to surface feed (Pearson & Parker 1973). On their Arctic breeding grounds, most scolopacids capture tundra insects by pecking, jabbing and probing (Holmes 1966), but Sanderlings seldom employ probing in northern wintering grounds (Burger et al. 1979). At Ouskip, the primary modes of foraging

employed by Sanderlings were stitching, jabbing and probing. Although captive White-fronted Sandplovers have been observed stitching, territorial White-fronted Sandplovers at Ouskip were 'peckers' throughout the year. That they can stitch as well suggests that they might need to use this method in particular situations. The preferred use of pecking as a feeding method usually reflects the requirement of large search areas and low bird densities (Pienkowski 1979, 1983a, 1983b). This observation is consistent with the territorial habits evident in the Ouskip White-fronted Sandplovers. Flocks of non-territorial juvenile White-fronted Sandplovers which appeared on occasions in the study area fed during the lower tidal times using predominantly jabbing and probing.

The patterns observed for Ouskip Sanderlings and White-fronted Sandplovers fall into what Pienkowski (1981) terms the 'plover strategy' and the 'sandpiper strategy'. He concluded that no one strategy is superior to the other over the complete spectrum of environmental conditions encountered. It seems logical that the high diversity of foraging tactics in Sanderlings can be maintained as an adaptation to a high diversity of feeding conditions encountered at breeding and wintering grounds and along migration routes. Both species as studied at Ouskip are clearly able to shift their foraging methods, and the choice of method is a function of the moisture content of the sand and the type of prey available in that foraging zone. Probing and stitching are employed in moist sand to capture subterranean prey, and pecking is used in drier microhabitats to catch surface-dwelling prey.

3.4.4 Aggression: competition or co-existence?

Competition (Gause 1934; MacArthur 1972) and avoidance (Morse 1974) are often implicated as being important mechanisms in resource partitioning in ecological communities (Schoener 1974). For example, Recher (1966) suggests that wintering shorebirds minimize competition for food through a combination of spatial and temporal segregation. However, Burger et al. (1977) found that shorebirds overlap considerably in both diet and feeding modes. Intra- and inter-specific aggression play important roles in shorebird spacing patterns on their wintering grounds, and have often been assumed to be indicators of competition (Thomas & Dartnall 1971; Burger et al. 1979; Myers & Myers 1979; Myers 1980a; Myers & McCaffery 1984). With intra-specific interference there should be a more equal use of the resource spectrum (Duffy et al. 1981), and such spacing suggests the possibility of competition during the evolutionary history of the species, or during periods of food shortage when optimal use of space is critical to survival (Herrera 1978).

White-fronted Sandplovers at Ouskip defended sectors along the shore, throughout the year. These territories are centred on the upper regions of the shore, where territories are apparently more easily maintained (Myers et al. 1979). There is a record of the same pair using a territory for eight years (W.J. Lawson, SAOS Nest Record Cards). In all instances in which one or both members of a territorial pair are permanently removed from territories, as at Silverstroom, and near Durban (W.J. Lawson SAOS Nest Record Cards), they were replaced, but not within less than a month. Since there are no documented records of non-territorial White-fronted Sandplovers breeding, and that birds wander from their territories only during the non-breeding season (Summers & Hockey 1980), these territories are clearly essential

to breeding (Crowe & Crowe 1984). Intra-specific aggression is also much more intense during the breeding season (W.R. Siegfried unpubl. data). Moreover, during the non-breeding season, non-territorial flocks of White-fronted Sandplovers are tolerated by territory holders, provided they do not intrude into the higher intertidal areas and feed during the lower tides (Summers & Hockey 1980).

Territories in non-resident wintering shorebirds are generally defended against conspecifics only (Hamilton 1959; Myers et al. 1981). For Sanderlings in California, the consistency of defence varied temporally (Myers 1980b; Myers et al. 1981). Myers et al. (1981) found that some Sanderlings defended intra-specific territories on a sandy beach at intermediate prey densities during high tides. However, at low tide, they foraged at adjacent harbour flats. Although Myers et al. (1979) and Myers & McCaffery (1984) have suggested that intra-specific territories should not be evident if food is superabundant, the only incidents of intra-specific aggression between foraging Sanderlings which I have observed were when prey was locally superabundant (Chapter 4), and therefore worth defending.

In the inter-specific aggressive encounters observed during this study, Sanderlings were always subordinate to White-fronted Sandplovers. These encounters were less frequent than one might have expected based on studies of shorebirds (e.g. Recher & Recher 1969; Burger et al. 1979). In fact, White-fronted Sandplovers spent much less time chasing Sanderlings from their foraging areas, than they did in intra-specific aggressive encounters with their neighbours (W.R. Siegfried unpubl. data). This suggests that avoidance through evolved preference for

different niches may have decreased the frequency of inter-specific encounters. This is, however, impossible to test (Branch 1984), especially since Sanderlings show such a variety of feeding habits over their wintering ranges. Instead, it is more likely that Sanderlings have retained the plasticity to be generalists, adjusting their foraging strategy to the prevailing conditions.

By definition, competition implies limiting or potentially limiting resources (Miller 1967). Assuming that food or some resource(s) were limiting at Ouskip, aggression should be positively related to bird densities. Although the density of White-fronted Sandpipers was essentially constant, densities of Sanderlings increased prior to migration without any apparent increase in intra- or inter-specific aggression, although Sanderlings extended their spatial and temporal ranges during this time. Only when spatial and temporal overlap coincided was this aggression observed, and this was independent of bird density.

Many southwestern Cape mudflats and sandy beaches are highly productive in terms of invertebrate prey (Puttick 1979; Bally 1981), and thus shorebird food appears not to be limiting overall. Further evidence of the lack of competition amongst wintering shorebirds has been demonstrated in several studies. Grant (1981), working in South Carolina, and Quammen (1980, cited by Duffy et al. 1984) working in California, have documented minimal changes in prey numbers during the wintering periods. Strauch and Abele (1979) in Panama, and Duffy et al. (1981), in Peru, also found no evidence of competition in wintering shorebirds. Duffy et al. (1981) demonstrate that food was not limiting in Peru, and question the use of inter- and intra-

specific territoriality as indicators of competition (cf. Myers and McCaffery 1984).

At Ouskip there is a relatively simple, essentially a two-species shorebird community, a small resident territorial species and a somewhat larger migrant non-territorial species. Resident birds in inter-specific contacts always succeeded in displacing migrant birds, and territory holders dominated non-territory holders whether conspecific or not. Therefore, what are the possible effects of these species on each other? Miller (1963) and Myers (1980c) have suggested that migrants may have an adverse effect on breeding in resident bird communities. However, Skutch (1950) and Moreau (1950) doubt that the breeding seasons of tropical birds are more influenced by migrant birds than by the abiotic environment. If high densities of Sanderlings were adversely affecting White-fronted Sandplover breeding activity, White-fronted Sandplovers should not breed during the austral spring and summer, yet they do. The likelihood of competition, for food anyway, is remote, since there is a flush of insect life at this time, allowing resident White-fronted Sandplovers to breed successfully (Chapter 5). If White-fronted Sandplovers in the southwestern Cape were seriously impacted by Sanderlings, they should spend more time foraging than roosting and preening, but they do not. Perhaps, as Moreau (1952) has suggested, migrants (Sanderlings) are sharing a superabundance of food with residents (White-fronted Sandplovers), or migrants are exploiting food which cannot (or need not) be used by the residents (Slud 1960; Morel & Bourlière 1962; Cox 1985). I doubt that the relatively longer-billed (Chapter 2) Sanderlings are being forced to forage sub-optimally during summer. Indeed, although the areas in which they forage,

at Ouskip, are exposed for unpredictable periods during the austral winter, Sanderlings leave the southwestern Cape at that time to exploit the superabundant food on their breeding grounds. This exploitation of seasonally superabundant resources, is one of the primary factors favouring the evolution of bird migration (Salomosen 1955; Morel & Bourlière 1962; Cox 1968; Lack 1968; Herrera 1978; Schneider 1981).

3.5 Summary

The foraging behaviour of Sanderlings Calidris alba and White-fronted Sandplovers Charadrius marginatus was studied at a sandy beach at Ouskip, Cape Province, South Africa during January 1977 to February 1978. Both species exhibited a tidal cycle in foraging activities, rather than a diurnal cycle. White-fronted Sandplovers tended to feed during the latter half of the tidal cycle (i.e. mid to high tide), whereas Sanderlings fed during the first half of the cycle (i.e. low to mid tide). Both species' foraging activity also varied spatially. White-fronted Sandplovers fed primarily in drier microhabitats above high tide level, and Sanderlings in wetter microhabitats near the water's edge. Inter-specific aggression was observed wherever there was both spatial and temporal overlap between the species, invariably resulting in Sanderlings being displaced. Temporal and spatial aspects in the foraging activities of both species varied seasonally in response to variation in the environment and the species' physiological requirements. Sanderlings spent more time feeding before and after migration, and fed in a greater variety of microhabitats. White-fronted Sandplovers increased their feeding time during the austral winter, when they used a broader range of sandy microhabitats and ephemeral freshwater ponds.

Intra-specific aggression among Sanderlings only occurred during instances of localized high prey density. White-fronted Sandpipers were territorial throughout the year, and vigorously defended their territories against conspecifics. They also occasionally chased foraging Sanderlings, from their territories. Each species had characteristic foraging methods, related to utilization of different microhabitats and prey, White-fronted Sandpipers tended to forage in the drier microhabitats and Sanderlings in the wetter microhabitats. Since changes in spatio-temporal patterns of habitat use appear to be the result of changes in the birds' physiological requirements, and in the environment, rather than the presence or absence of either species, I conclude that competition is not in operation at Ouskip. Competition may have played an important role in the evolution of the patterns which were observed during this study.

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APPENDIX 1

PREY OF WHITE-FRONTED SANDPLOVERS AND SANDERLINGS, AS REFLECTED BY OESOPHAGUS AND STOMACH
 CONTENTS OF BIRDS COLLECTED AT SILVERSTROOM BETWEEN FEBRUARY 1977 AND JANUARY 1978

Category	White-fronted Sandplover (n = 51)	Sanderling (n = 72)
Surface prey:		
<u>Talorchestia capensis</u> (2-12mm)	^a Feb, Mar, Apr, May, Jun, Jul, Aug, Nov, Dec	^b Mar, Apr, Sept
Kelp flies (3-6mm)	Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec, Jan	Apr, May, Sep
Coleopterans (3-7mm)	Sep, Oct, Nov, Dec	Mar, Apr, Sep
Unident. insects (3-5mm)	Sep, Oct, Nov, Dec	Sep, Oct
Unident. Insect larvae (3-5mm)	Sep, Oct, Nov, Jan	Sep, Oct
Subterranean prey:		
<u>Eurydice longicornis</u> (2-5mm)	Jun, Jul, Aug, Sep	Feb, Mar, Apr, May, Sep, Oct, NOV
<u>Tylos granulatus</u> (2-8mm)	Mar	Mar
<u>Pontogeloides latipes</u> (2-6mm)		Feb, Mar, Apr, May, Sep, Oct, Nov, Dec, Jan
<u>Exciroliana natalensis</u> (2-5mm)	Jun, Jul, Aug, Sep	Feb, Mar, Apr, May, Sep, Oct, Nov, Dec, Jan
<u>Scololepus squamata</u> (11-22mm)	May, Jun, Jul	Feb, Sep, Oct, Nov, Dec, Jan
<u>Gastrosaccus psammodytes</u> (3-14mm)	Jun, Jul, Aug, Sep	Oct, Nov, Dec, Jan
<u>Donax serra</u> (3-5mm)		Feb, Mar, Apr, Oct, Nov, Dec
Oligochaetes	Mar, Apr	Mar, Apr

^a approximate size range for whole animals

^b months in which category was present in oesophagus and/or stomach

CHAPTER 4

VARIATION IN THE SIZE AND STRUCTURE OF FLOCKS OF SANDERLINGS

4.1 Introduction

Grouping patterns of foraging Sanderlings (Calidris alba) vary geographically and locally (Burger et al. 1979; Myers 1979, 1980, 1983; Myers et al. 1979a, 1979b, 1981). In southern Africa, Sanderlings winter along open sandy beaches, and are generally non-territorial and forage in flocks (Pringle & Cooper 1977; Maclean 1985). It has been suggested that predators are a major selective force promoting flock-foraging in intertidal shorebirds (Page & Whitacre 1975; Myers 1980, 1984). For Sanderlings, Silliman et al. (1977) hypothesized that flock foraging allows individuals to spend relatively less time watching for predators between foraging movements, thereby allowing more time for foraging (Krebs 1973; Thompson et al. 1974). However, Murton (1971) and Goss-Custard (1980) maintain that, although flocking aids birds in locating and exploiting food sources, feeding efficiency of individuals within large flocks is decreased due to an increase in interference. Since my own observations, and those of colleagues who have studied shorebirds in southern Africa, have not produced records of predators attempting to prey on foraging Sanderlings, this study was directed at investigating foraging-related hypotheses.

4.2 Study area and methods

The study area was a 1.5-km stretch of exposed sandy beach bounded at one end by rocky outcrops at Ouskip (33 44'S 18 26'E), approximately 25km north of Cape Town (Fig. 4.1). Flock size of foraging Sanderlings was monitored during three successive days

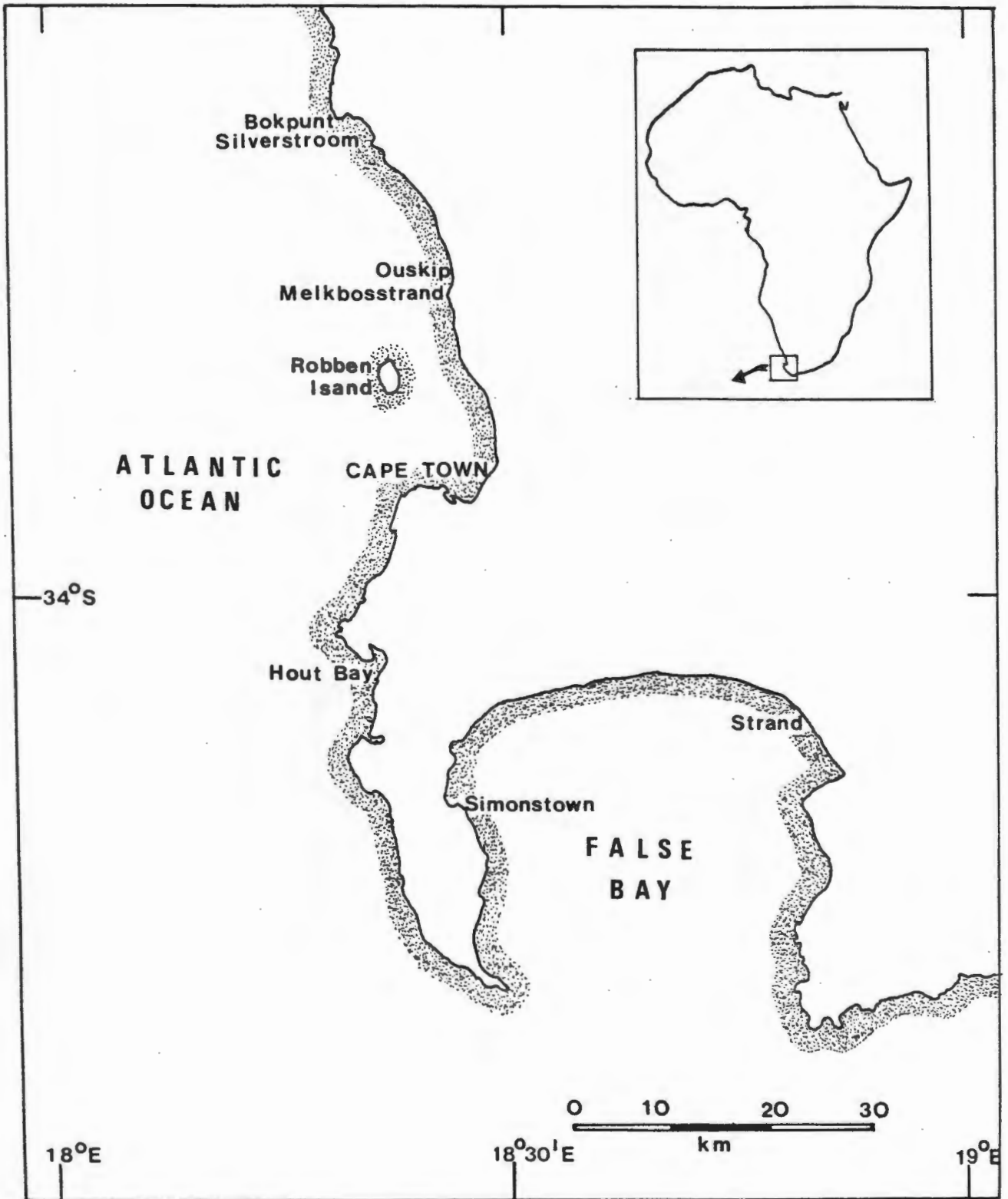


FIGURE 4.1

The southwestern Cape Province, South Africa, showing the location of the Ouskip study area

in December 1978, during which there was fair weather with low wind. Flock sizes were monitored during the three hours before and three hours after low tide (Fig. 4.2). Variation in flock sizes throughout the year were also recorded. Flocks were taken to be groups of birds within approximately 20 bird-lengths of each other, since my research during the previous seven months indicated that this was the maximum inter-bird distance for groups which moved in a cohesive fashion. The compactness of flocks was measured (in terms of mean bird-lengths) over tidal time and foraging in different microhabitats, and the proportion of feeding birds observed in each flock was also recorded. For 38 flocks, the density of potential subterranean invertebrate prey in the immediate vicinity of the groups was sampled using a plastic corer (50mm in diameter) to a depth of 60mm. Invertebrate data were collected immediately after flock size, spacing and foraging information had been noted. The birds were chased from the area and 20 cores were taken randomly within the foraging area. The sand from the cores was then sieved (through a 1mm sieve), and all the invertebrates collected were counted and identified to species level.

The following microhabitats were recognized: zone A - directly at the water's edge; zone B - wet area approximately 0.3m from A; zone C - wet area covered by water film; zone D - damp sand no water film; zone E - drift line; and zone F - dry sand. These zones were scored from 1 (zone A) to 6 (zone F) for dryness of sand to allow for statistical analysis of flock size in relation to moisture of the substratum. Five categories of foraging methods were recognized: taking an organism from the surface of the substratum (pecking); inserting the bill into the substratum, for less than half its length (jabbing); inserting

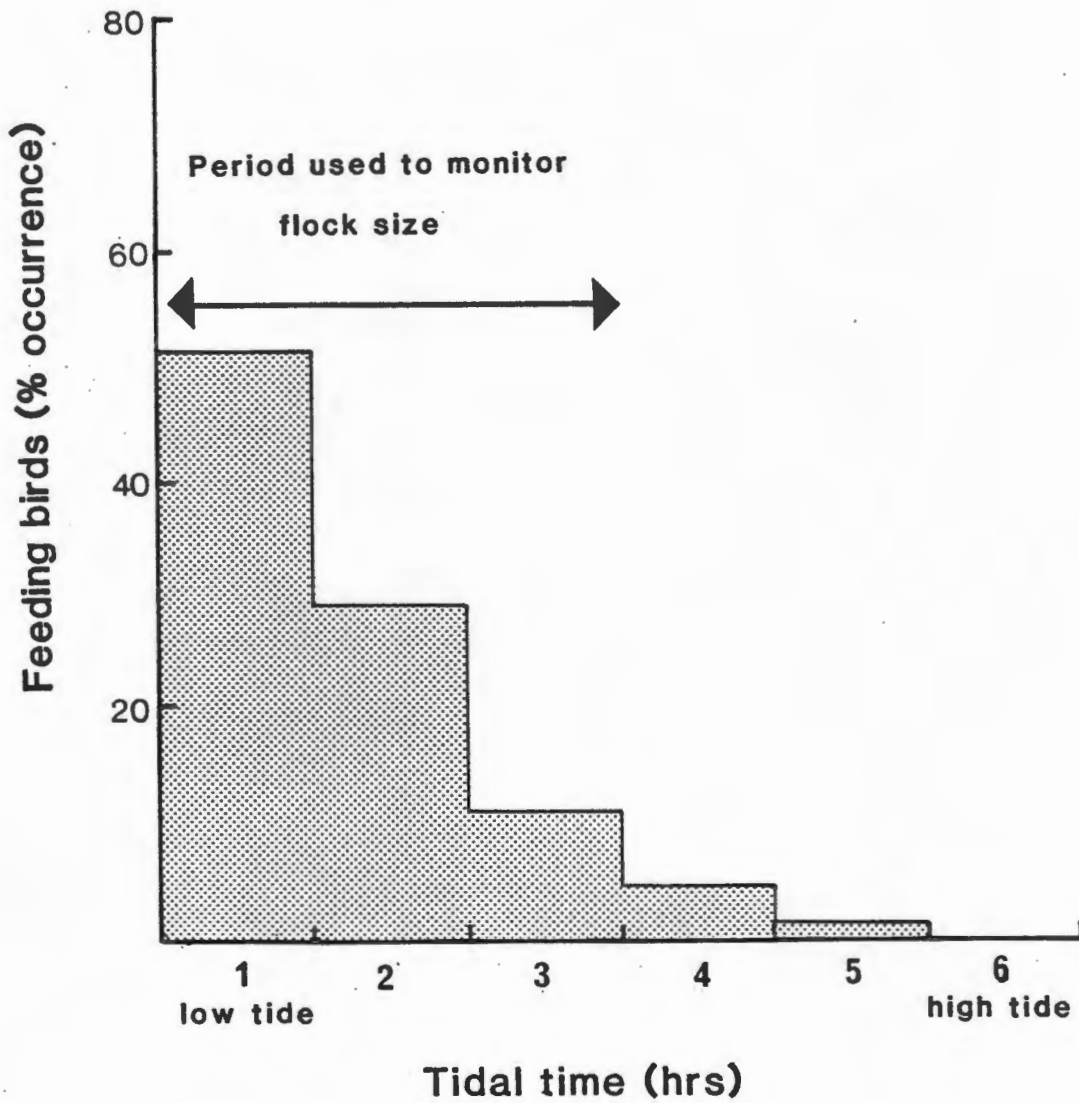


FIGURE 4.2

Occurrence of feeding Sanderlings in relation to tidal time, showing the tidal period during which flock size was monitored

the bill into the substratum for more than half its length (probing); a rapid probing motion during which the bill is quickly removed during each successive probe (stitching, sensu Burton 1974); and a similar rapid movement except that the bill is not removed between each successive probe (ploughing). Variation in spatial and temporal use of the intertidal habitat and in foraging methods by Sanderlings is treated in Chapter 3.

4.3 Results

Ouskip Sanderlings did not have a single optimal flock size (Fig. 4.3). The frequency distribution of flock sizes was bimodal, with a peak at small flock sizes and another at large flock sizes. Large flocks of foraging Sanderlings tended to run along the water's edge, and then split into smaller groups within which the birds fed in bouts of a few minutes before coalescing again into large flocks. In other words, large flocks contained proportionally fewer feeding members than small flocks ($\underline{p} < 0.001$; \underline{t} test; Figs 4.3 & 4.4). In large flocks (i.e. more than 50 birds) there was a significant negative relationship between flock size and subterranean prey density ($\underline{r} = -0.495$; $\underline{p} < 0.05$); Fig. 4.4). There was no such relationship for small flocks (i.e. fewer than 50 birds). Thus, flocks were characterized as either searching (having less than 50% of members feeding) or feeding (having greater than 50% of their members feeding), according to the number of feeding members in each flock observed (Figs 4.3 & 4.4). This bimodal pattern of flock size distribution was evident throughout the year, although the absolute flock size varied (Fig. 4.5).

Intra-specific aggression was observed on only one occasion (Fig. 4.4), when the density of an important prey species (the

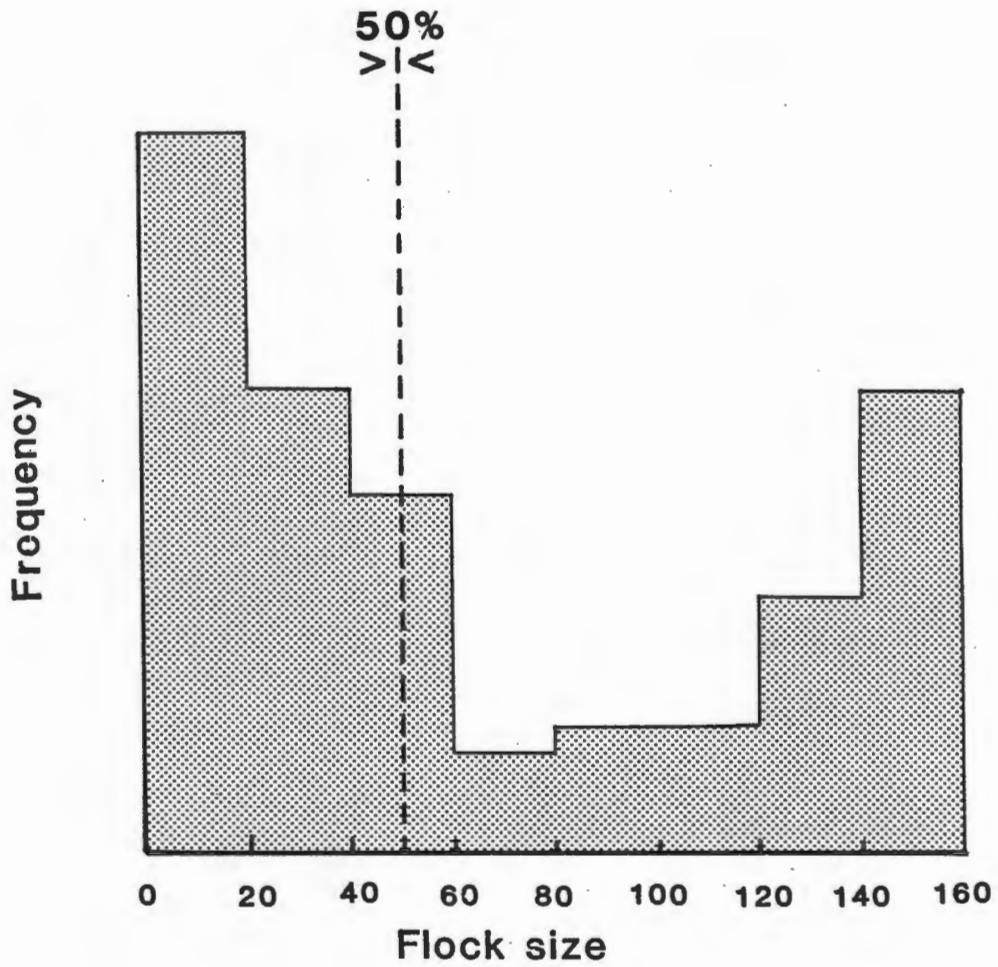


FIGURE 4.3

The size frequency of Sanderling flocks at Ouskip, during December 1978. Dashed line separates flocks with > 50% of their members feeding from those with < 50% of their members feeding

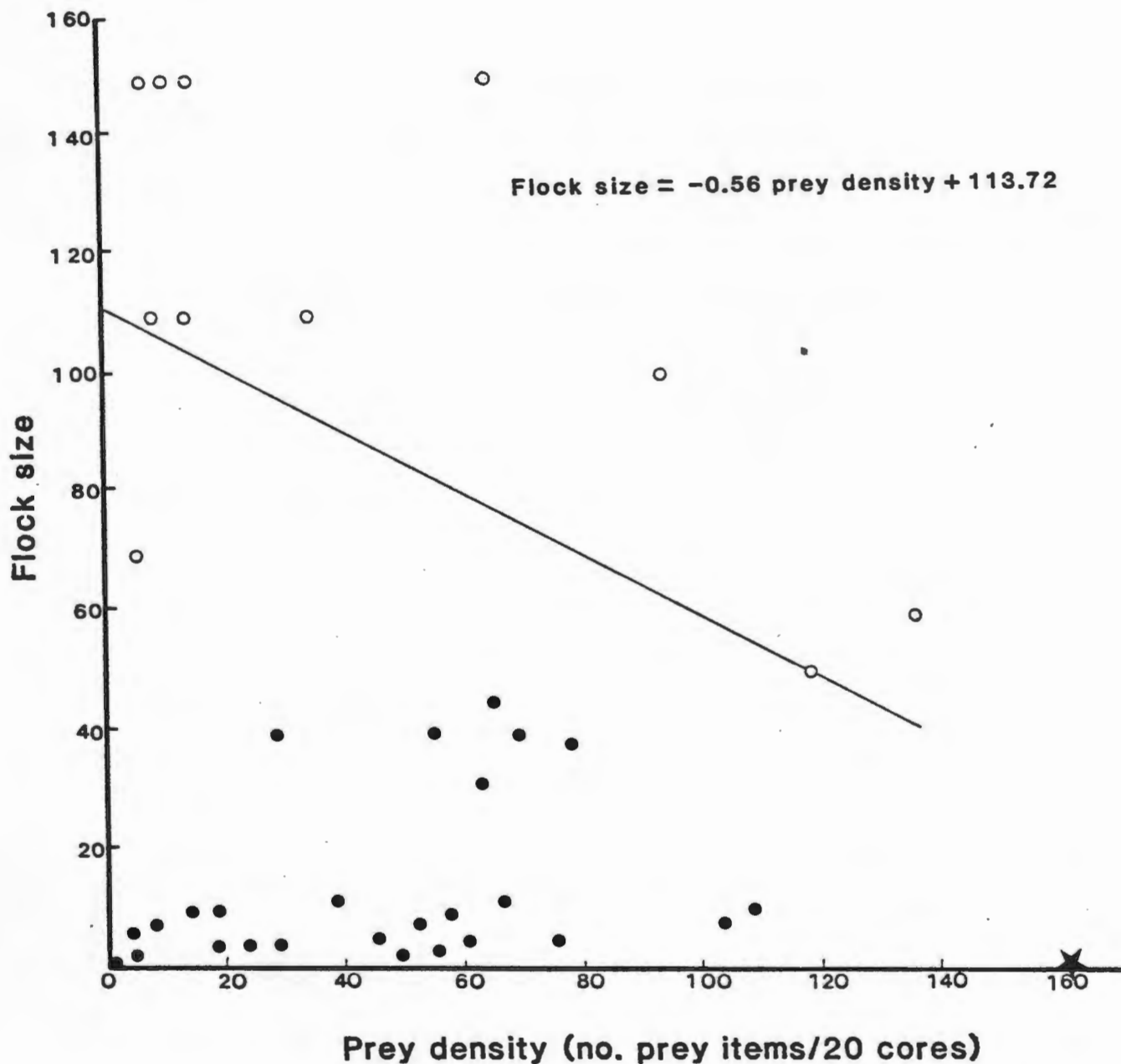


FIGURE 4.4

Sanderling flock size in relation to invertebrate prey density.

○ = flocks with < 50% of their members feeding, ● = flocks with >

50% of their members feeding, ★ = 'territorial' individuals

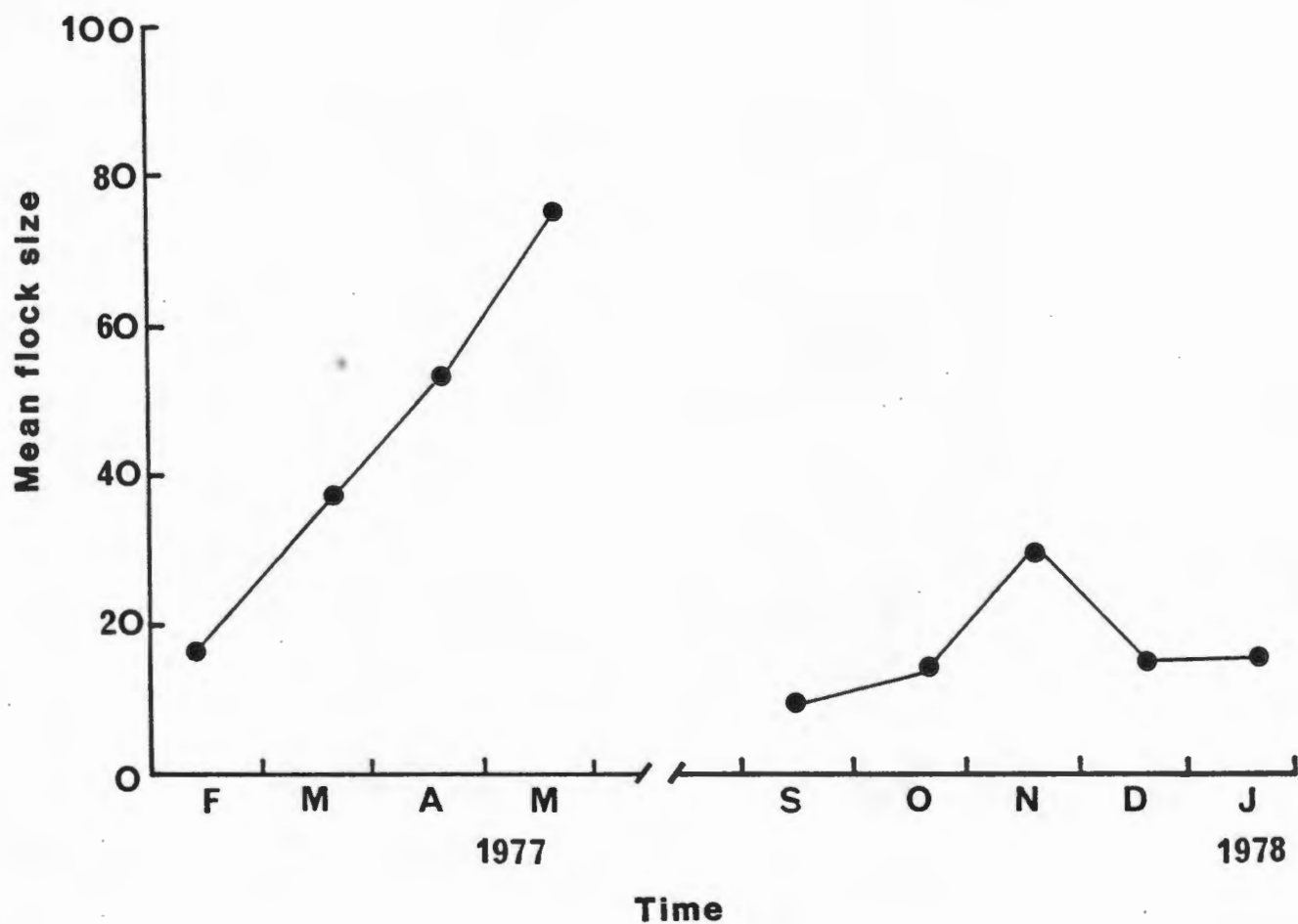


FIGURE 4.5

The mean size of Sanderling flocks at Ouskip, February 1977 to January 1978. Dashed line separates flocks with > 50% of their members feeding from those with < 50% of their members feeding

polychaete worm Scololepus squamata was in excess 160 prey items per 20 core samples (approximately 15 times greater than normal density). On this occasion, within a 20-minute period, 12 aggressive encounters were recorded. In these encounters, the 'intruder' always retreated, and the dominant bird appeared to defend an area in which it fed.

Mean inter-bird distance was positively correlated with tidal time (Fig. 4.6; $r = 0.82$, $P < 0.01$) and with the dryness of the sand (Fig. 4.7; $r = 0.90$, $P < 0.01$). Thus, Sanderling flocks became less compact as birds foraged at higher tides and in drier microhabitats. Moreover, the predominant modes of feeding changed from stitching and probing to probing and pecking (Figs 4.8 & 4.9) as flocks became less tightly packed. To summarize, Sanderling flocks became less compact and used different modes of foraging as they moved away from the tidal times and microhabitats in which they normally concentrated their feeding activities (Chapter 3; Figs 4.6 & 4.7).

4.4 Discussion

Two classes of hypotheses have been offered for variation in group size in animals. The first class of hypotheses concerns advantages to the animals as prey and the second advantages to the animals as predators (Bertram 1978; Rubinstein 1978). To date, the effects of predators on shorebird grouping patterns have been studied primarily in the northern hemisphere (see Myers 1984). Goss-Custard (1970) investigated flocking in shorebirds with respect to both predation and foraging effects, and the relationships between the two effects. He concluded that these effects were possibly not mutually exclusive and that laboratory and field tests were needed to test this view. Page and

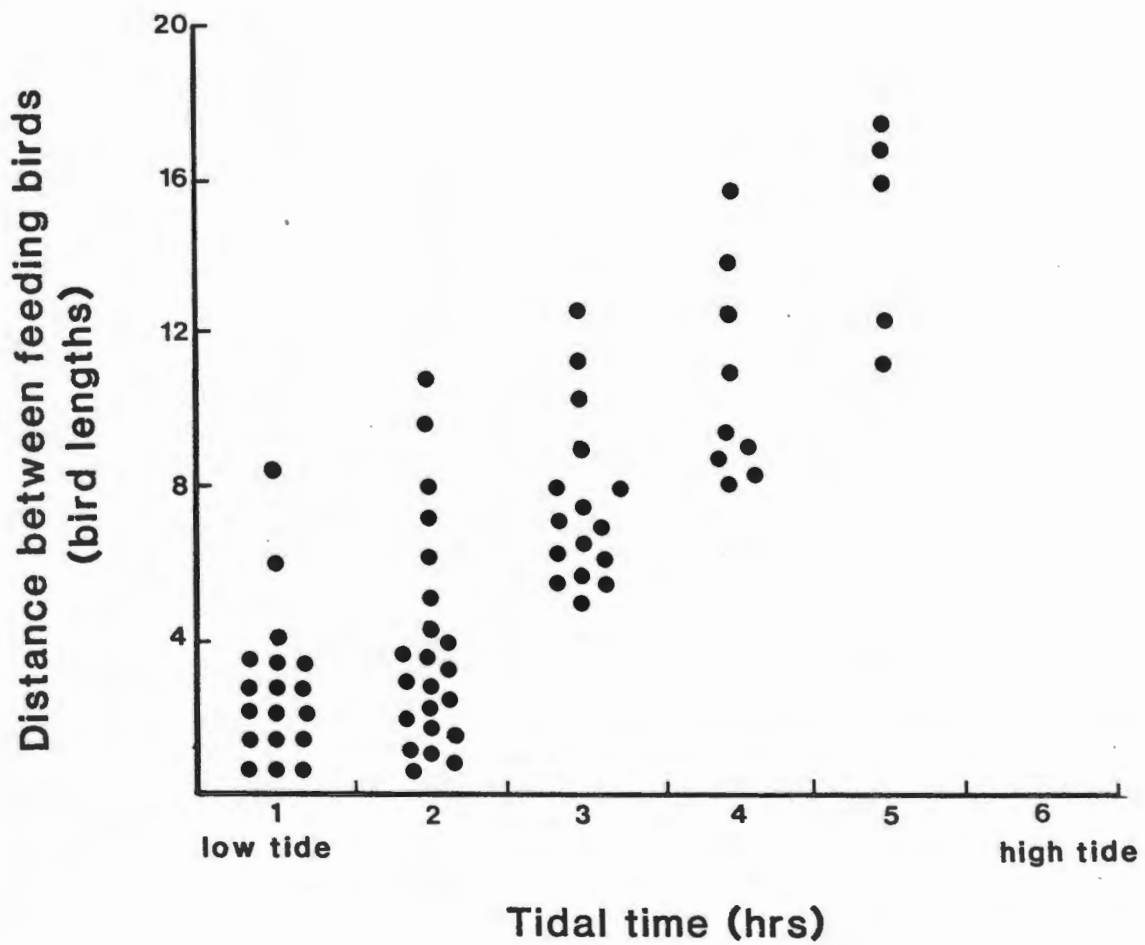


FIGURE 4.6

Variation in the compactness of Sanderling flocks in relation to tidal time

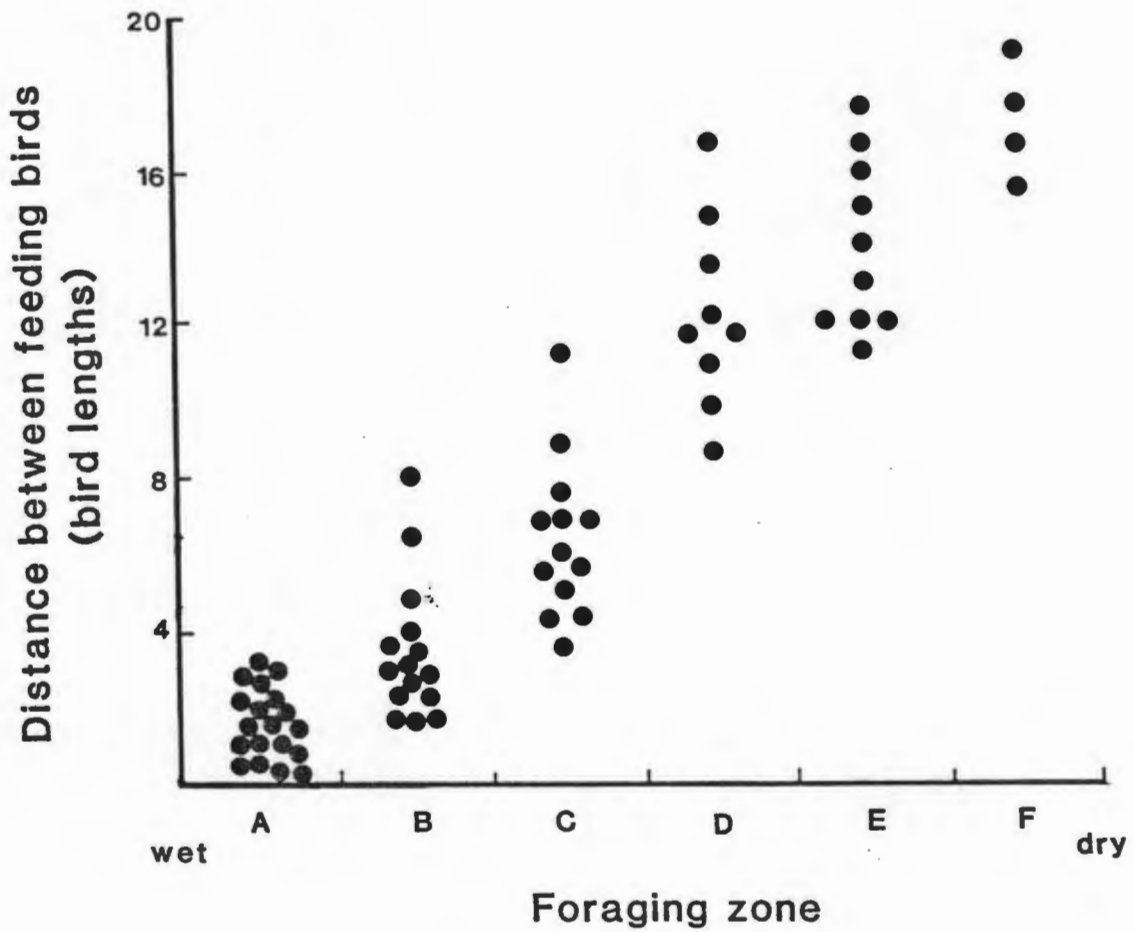


FIGURE 4.7

Variation in the compactness of Sanderling flocks in relation to foraging zone

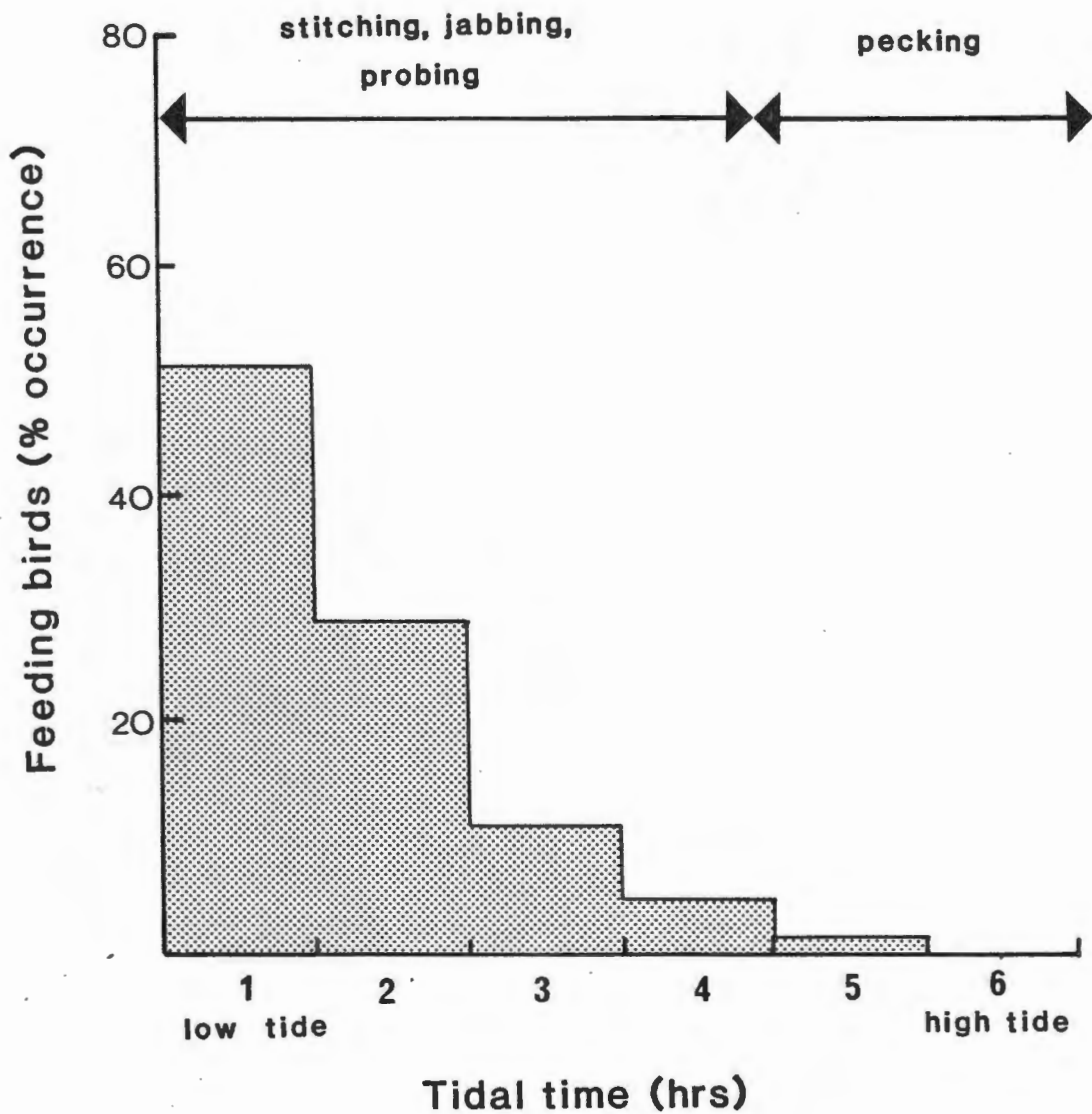


FIGURE 4.8

Foraging activity of Sanderlings in relation to tidal time and the main foraging methods employed during the tidal cycle

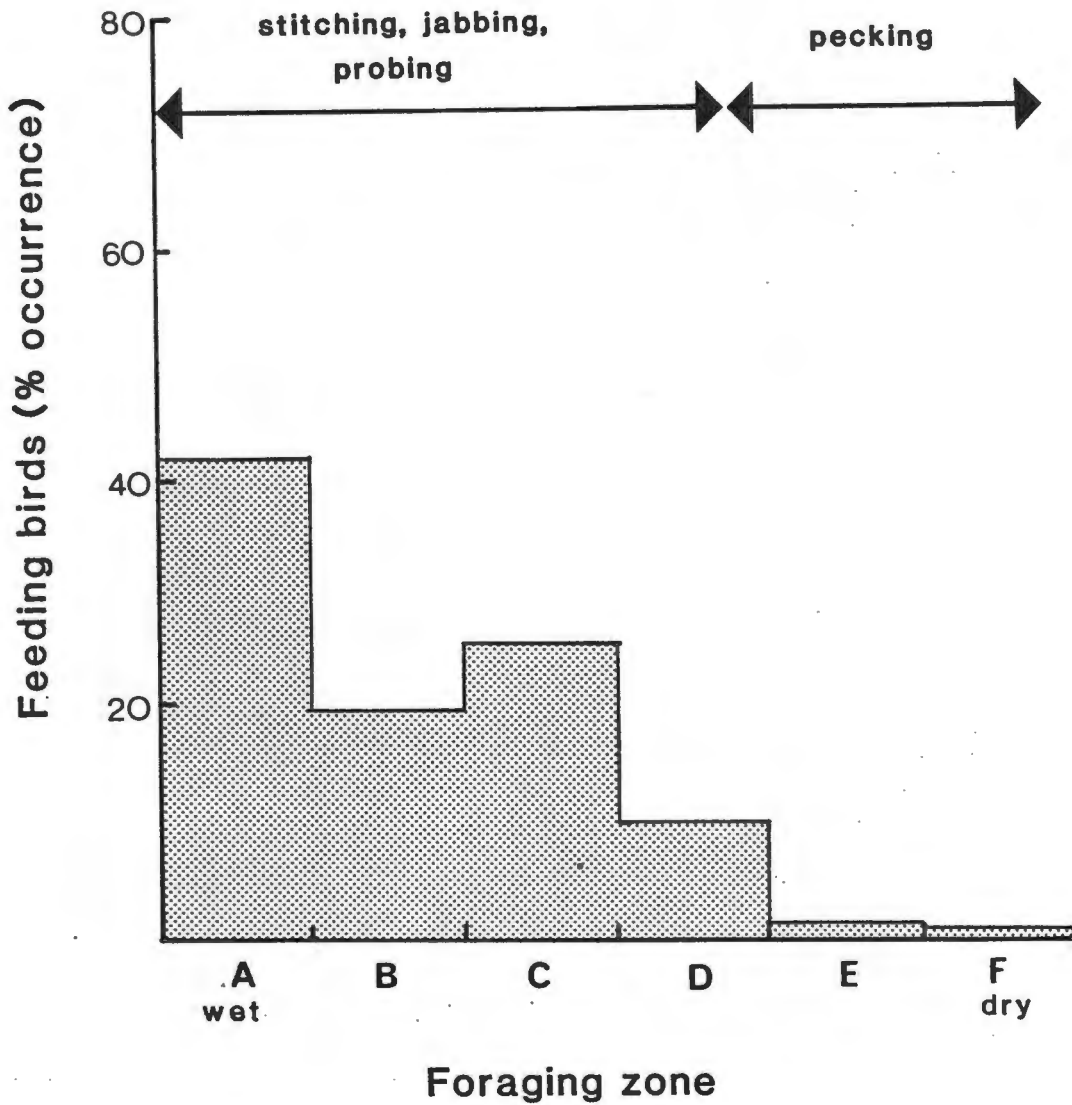


FIGURE 4.9

Feeding activity of Sanderlings as a function of foraging zone and the main foraging methods used in these zones

Whiteacre (1975) demonstrated the importance of predation by showing that a substantial portion of shorebirds wintering in California are killed by raptors, and that the probability of a lone bird being taken by a raptor was significantly greater than that for a bird in a flock. In a second study, Myers (1980) observed Sanderlings either in flocks or as single territorial birds. However, when a Merlin Falco columbarius took up residence in his study area, Sanderlings associated only in flocks, which became larger and more compact (Myers 1984). Unfortunately, I was unable to test any predator-avoidance hypothesis, since there is little evidence for diurnal raptors preying on shorebirds along marine shores in southern Africa. Thus, there must be some other explanation for the consistent bimodal grouping pattern observed for Sanderlings at Ouskip.

An often cited prey-detection hypothesis concerning grouping in animals is that of the Information Centre (Ward & Zahavi 1973). An Information Centre is either a communal roosting or nesting area at which an unsuccessful forager can observe and follow others who appear to have been more successful. Myers (1983, 1984) discounts the applicability of this hypothesis for Sanderlings, accepting the null hypothesis of random association at roosts and within foraging flocks. However, Smith and Stiles (1979) reject the random-association hypothesis for migrant and wintering Western Sandpipers C. mauri in Costa Rica. Data from southern African Sanderling populations suggest that there is little exchange between populations feeding on nearby beaches (Pringle & Cooper 1977), and that birds which winter in an area in one year tend to return to the same area in subsequent years (R.W. Summers et al. in litt.). However, until many more data are available as to associations between individually identifiable

members of roosting and foraging flocks, the applicability of the Information Centre hypothesis to Sanderling groupings in the southwestern Cape remains untestable.

The one factor common to both the predator- and the prey-detection hypotheses is the notion of at least an initial increase in success (at predator detection or prey capture) with increasing group size. Thereafter, success either continues to increase (Powell 1974), or decreases after reaching some optimum value (Siegfried & Underhill 1975). However, there appeared to be no single optimal flock size for Sanderlings at Ouskip. Moreover, the general pattern of large flocks breaking up into smaller flocks was consistent throughout the wintering season, although absolute flock size varied. Since, large flocks had fewer members feeding and were observed in areas with relatively low prey density, I suggest that at least one function of these large flocks is to locate patchily distributed subterranean food which abounds on southwestern Cape sandy beaches (Brown 1964; Bally 1981), especially in wetter microhabitats in which Sanderlings feed (Chapter 3). Once these patches are located, flocks split up into smaller flocks to feed. However, why should large flocks break up into smaller feeding flocks once food patches have been detected?

Goss-Custard (1980) and Myers (1980) suggest that flocking in shorebirds might decrease the per capita feeding rate through direct (e.g. aggression) or indirect (e.g. local depletion of prey) interference; and interference should vary with foraging style (Goss-Custard 1970, 1976; Rands & Barkham 1981). Intra- and inter-specific aggression which results from local depletion of prey (Recher & Recher 1969; Silliman et al. 1977), should be

greatest amongst those shorebirds which can assess prey distribution/availability readily, i.e. in those species which use visual cues to capture prey (Burger et al. 1979). I discount intra-specific aggression as an important factor for Sanderlings at Ouskip, since overt aggression was observed within foraging flocks on only one occasion during my 13-month field study. Moreover, this intra-specific aggression occurred at a patch with abnormally high prey concentrations. I therefore suggest that, although food was not an overall limiting resource within the zones used by Sanderlings for foraging, localized patches of food are depleted or disturbed relatively rapidly, thereby limiting the optimal size of foraging flocks. Puttick (1980) has also suggested that flocking in Curlew Sandpipers C. ferruginea wintering in the southwestern Cape is a response to optimal foraging conditions, and that food also is not limiting. Why then has intra-specific aggression been observed in wintering Sanderling populations elsewhere?

Recher and Recher (1969) observed aggression in Sanderlings using pecking to capture egg-masses of the Horseshoe Crab Limulus polyphenus on the surface. Burger et al. (1979) also found that inter- and intra-specific aggression in shorebird flocks for species employing probing as a predominant mode of foraging, and noted an increase in aggression in 'non-probers' foraging above the water's edge, were seldom observed. Goss-Custard (1970, 1976) attributes increases in aggression to the fact that, when prey are detected by visual cues, flocking would interfere with prey capture. This is analogous to my hypothesis that large flocks of Sanderlings might either deplete prey stocks locally, causing the prey to become less available, or indirectly interfere with the foraging activity of neighbouring birds.

Inter-bird distances in Ouskip Sanderlings should increase with a shift from subterranean to surface-dwelling prey, and they do. Inter-bird distances can be maintained by aggression or avoidance (Burger et al. 1979; Stinson 1977; Vines 1980), and should vary in relation to food density and predation risk (Myers 1984). Sanderlings wintering at Ouskip foraged during lower tides and captured their subterranean prey largely by probing, i.e. by tactile means (Chapter 3). Since flocking is advantageous as a means of locating patchy food supplies (Hinde 1961; Krebs 1973), but perhaps disadvantageous as a means of exploiting these patches, I hypothesize that the interference effects attending high bird densities, and foraging using visual cues, at higher tidal tides and levels, are circumvented through large flocks splitting up into smaller feeding groups.

In conclusion, although data for Sanderlings at Ouskip suggest that predators may not be an important factor influencing flocking, predation cannot be dismissed as an evolutionary force. Indeed, since the Sanderling has a nearly cosmopolitan wintering distribution (Voous 1960; Chapter 2), it presumably encounters many different levels of predation and foraging opportunities. Thus, flocking in Sanderlings appears to have evolved as the most efficient means of coping with a series of conflicting selective pressures.

4.5 Summary

The frequency distribution of foraging flock sizes for wintering Sanderlings on a southwestern Cape sandy beach was bimodal, with a peak at small flock sizes and another at large flock sizes. It is hypothesized that large groups of Sanderlings consist of individuals searching for prey, and small groups

consist of subsets of these larger groups which have located rich patches of subterranean prey. Moreover, since Sanderlings capture these prey by probing with the bill in the sand, this hypothesis does not apply to Sanderling flocks foraging on surface food, employing pecking to catch their prey. Under these circumstances, other flock members probably interfere with prey capture. Sanderlings minimize this interference by increasing the inter-bird distance between foraging flock members, using pecking as a means of prey capture.

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CHAPTER 5

VARIATION IN THE BREEDING SEASON OF THE WHITE-FRONTED SANDPLOVER
IN SOUTHERN AFRICA

5.1 Introduction

For many years, ornithologists have contributed information concerning the breeding biology of local birds to the Southern African Ornithological Society's Nest Record Card Scheme (N.R.C.S.). The N.R.C.S. has sufficient records for many species, so that quantitative studies of spatial and temporal variation in their breeding patterns may be attempted. As of June 1980, nest record cards for the White-fronted Sandplover (Charadrius marginatus), a resident monogamous (Summers & Hockey 1980) shorebird, numbered 1 308, and, on a geographical scale, cover much of the species' range in southern Africa (Maclean 1985; Chapter 2).

The aims of this paper are to answer the following questions:

1. Is there statistically significant geographical variation in the breeding season of the White-fronted Sandplover in southern Africa?
2. If so, is this geographical variation correlated with variation in rainfall, the environmental variable which apparently has a marked direct and indirect influence on the timing and success of breeding in many southern African birds (Moreau 1950; Benson 1963; Winterbottom 1963a; Liversidge 1966; Crowe 1978)?
3. Is there significant year-to-year variation in the breeding season of White-fronted Sandplovers within a given geographical area?
4. If so, does this variation follow shifts in rainfall

patterns?

5. What is/are the possible cause-effect relation(s) between breeding season variation in White-fronted Sandplovers and variation in their environment?
6. What aspects of the biology of this species are adaptations to opportunistic/seasonal breeding?

5.2 Methods

In quantitative analyses of the temporal variability of breeding and other seasonal phenomena, standard statistical tests (e.g. t and F tests, regression and correlation analysis, etc.; Sokal & Rohlf 1969) are usually invalid, since the domain (i.e. time) in such analyses is circular. In other words, on a yearly scale, day 365 (December 31) is not 365 times day 1 (January 1) and day 1 is 'closer' to day 365 than it is to day 5. However, the development of a computer programme, DIRECT (Mimmack *et al.* 1980), enables one to compare statistically data sets, such as breeding seasons, which have circular domains.

For each White-fronted Sandplover nest record, the approximate date on which the first egg was laid (D.F.L.) was estimated, and I arbitrarily took this day to be the commencement of breeding for the bird in question. In D.F.L. calculations, the incubation period was taken to be 30 days (Maclean 1985). The D.F.L. dates were then converted into approximate Julian day equivalents (day 1 = January 1st and day 360 = December 31st). These D.F.L. data were then grouped into geographical units (Fig. 5.1), which produced both reasonable sample sizes and a sufficiently fine-grained coverage of the southern African breeding range of the White-fronted Sandplover.

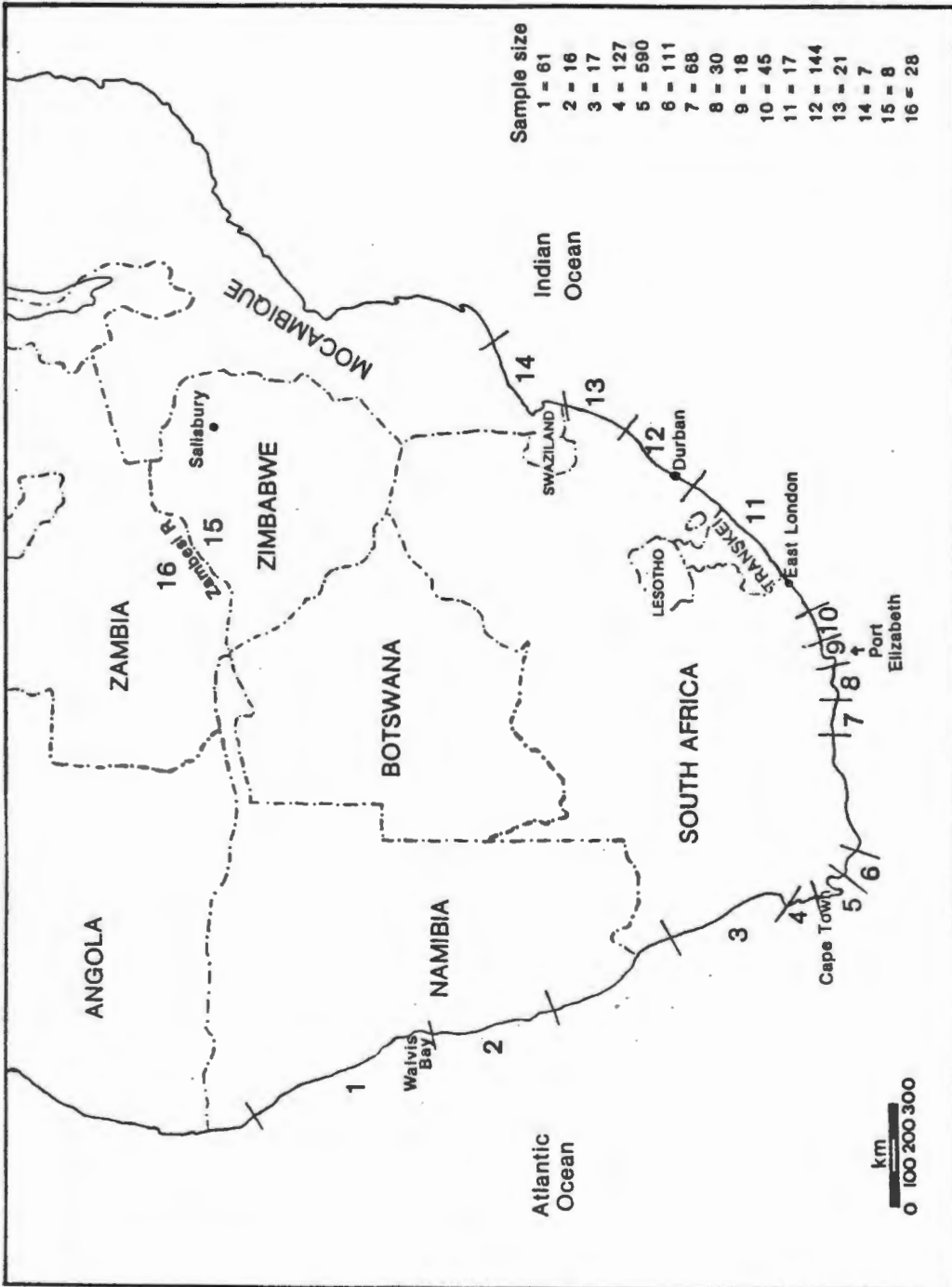


FIGURE 5.1

Map of southern Africa showing the geographical units used in this analysis, and the number of breeding records for each unit

For two of these geographical units, one (no. 4) in a winter rainfall area, the other (no. 12) in a region with summer rainfall, there were adequate data for several years, which allowed investigation of possible year-to-year variation in breeding season within a geographical area. The modal D.F.L., and its 95% confidence interval, were then calculated for each geographical unit, and for the data for each year for units 4 and 12, using DIRECT. The null hypotheses that the modal D.F.L. in the White-fronted Sandplover does not vary geographically, or temporarily, within units 4 and 12, were tested statistically using the same programme.

Data on long-term mean monthly rainfall, and on monthly rainfall for the years for which I investigated intra-unit year-to-year variation in breeding, were extracted from published records (Weather Bureau 1950, 1955-78; Thornthwaite 1962). Long-term monthly data were plotted as a contour map using a computer graphics package (Diedericks 1979), and superimposed over a plot of modal D.F.L.s for the 16 geographical units, to illustrate geographical variation in the D.F.L./rainfall relation. The modal vectors of rainfall (M.V.R.) for each of the 16 geographical units were obtained and compared to one another using DIRECT, to determine if there was geographical variation in patterns of rainfall. In order to test statistically that breeding in White-fronted Sandplovers is related to patterns of rainfall, I regressed modal D.F.L. against M.V.R. for the 16 geographical units. In this analysis, in order to eliminate the circularity of the domain, I added 360 days to all modal vectors with values less than 30.

To elucidate the functional relationship between breeding in White-fronted Sandplovers and temporal variation in the

environment, during 1977 - 1978, I collected environmental and ecological data at Ouskip (33° 44'S 18° 26'E) whilst observing the foraging and breeding behaviour of the resident population. These data which include: temperature, daylength, rainfall and potential food availability, were related to the breeding status of three of the four pairs of birds which were resident at Ouskip (Chapter 1).

5.3 Results

The results of analyses of patterns of geographical variation in the breeding season in the White-fronted Sandplover, and of patterns of variation in rainfall, are summarized in Figure 5.2. There was significant geographical variation in both modal D.F.L. and M.V.R. among the 16 geographical units [$Z = 56,6$, $\underline{p} < 0,005$; $Z = 1467,7$, $\underline{p} < 0,005$]. In South West Africa/Namibia White-fronted Sandplovers breed mainly during late summer (December-January). Moving southwards, from Langebaan Lagoon through the southwestern Cape, this species tends to breed in spring and early summer (September-November). Moving up the east coast of southern Africa from Durban northwards, populations tend to breed further into winter (July-August). Zimbabwean and Zambian White-fronted Sandplovers tend to breed slightly later, i.e. in August or early September. Examination of Figure 5.2 suggests that, along the southwestern and southern Cape coast, breeding follows soon after the wet season. Eastwards, and into the inland areas, breeding precedes the onset of the wet season (November-February). The relationship² between D.F.L. and M.V.R. is negative and highly significant ($\underline{r} = 0,61$; $\underline{p} < 0,001$; Fig. 5.3). In other words, White-fronted Sandplovers in southern Africa breed 'earlier' in the year as

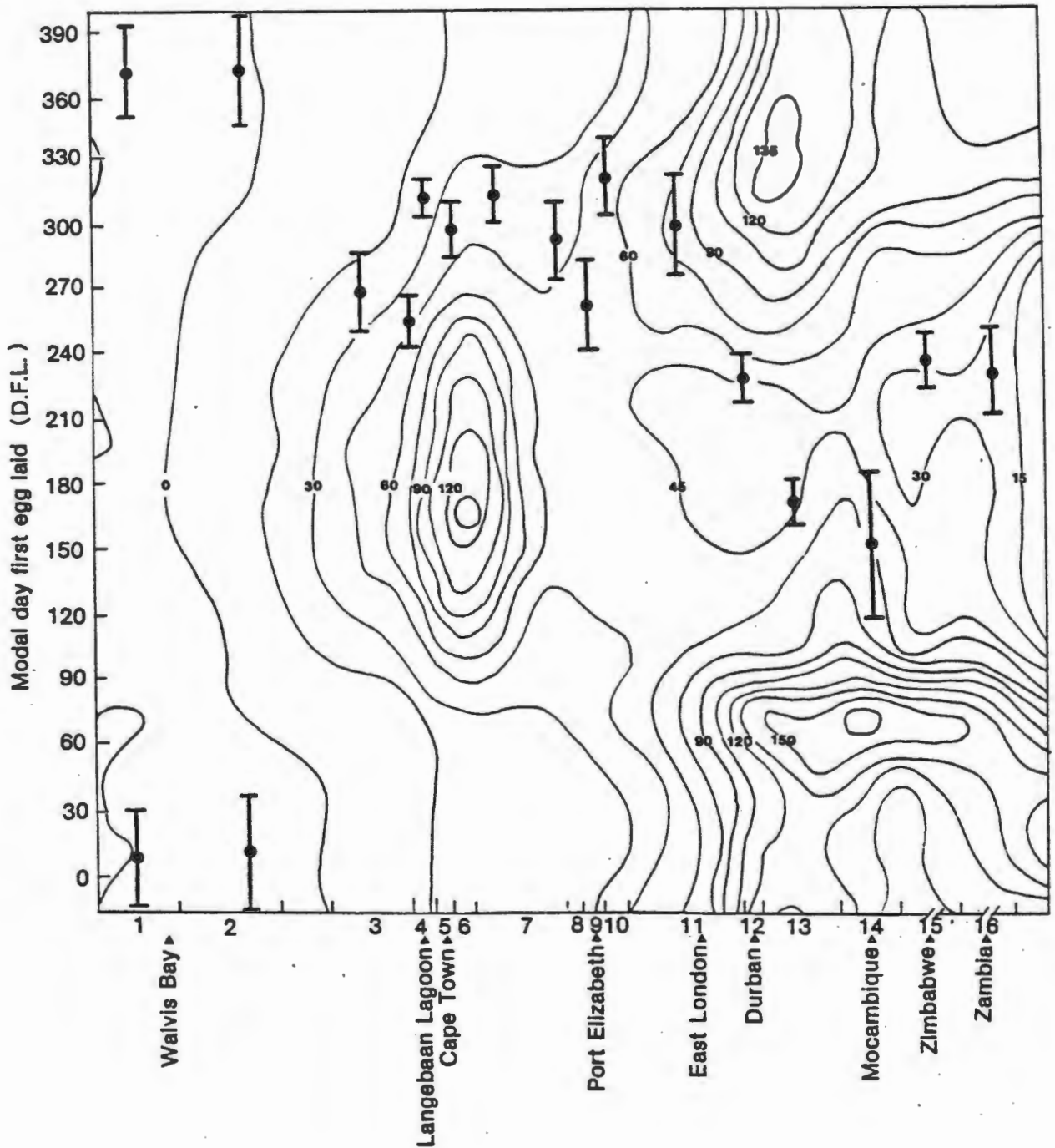


FIGURE 5.2

Geographical variation in modal day of first laid egg (D.F.L.) + 95% confidence intervals, and monthly isohyets for rainfall (mm), for the 16 geographical units in Fig. 5.1

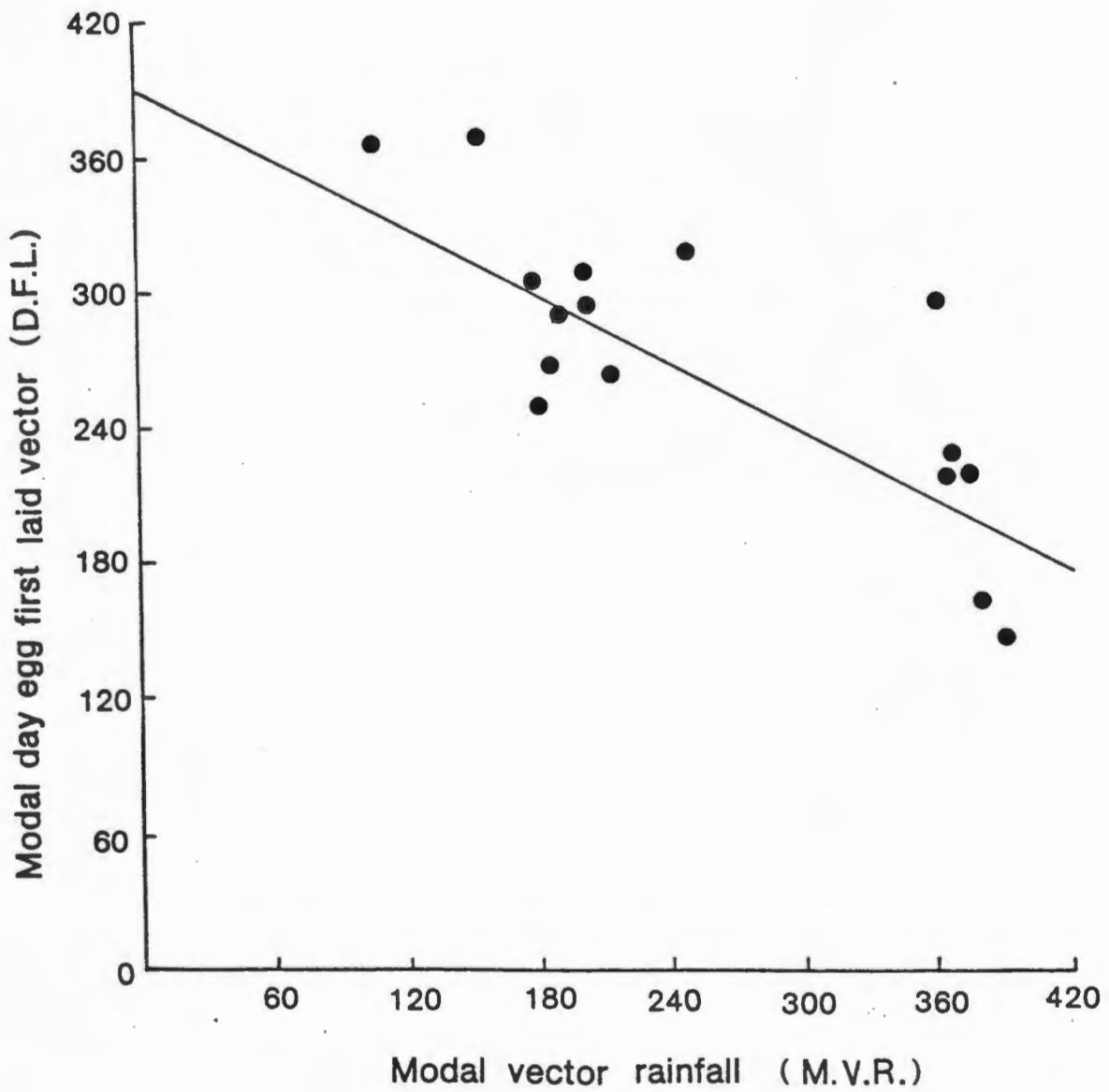


FIGURE 5.3

Plot of modal day of first laid egg (D.F.L.) vs. modal vector of rainfall (M.V.R.) for the 16 geographical units

rain falls 'later' in the year.

There is significant year-to-year variation in rainfall for both geographical units analyzed. There was no significant variation in White-fronted Sandplover breeding for unit 12 (Fig. 5.4). For unit no. 4, for which there was significant year-to-year variation in breeding, the modal D.F.L. tended to be earlier when the M.V.R. was also earlier (Fig. 5.5).

The first sightings of eggs in nests for the three pairs of White-fronted Sandplovers observed nesting at Ouskip occurred after a peak of invertebrate prey numbers in spring, and the invertebrate prey were most abundant following rainfall peaks (Fig. 5.6).

5.4 Discussion

Given that there is geographical variation in breeding, and year-to-year variation in breeding in a winter rainfall area, and that both types of variation seem to be related to patterns of rainfall, what is the possible cause-effect relationship between rainfall patterns and breeding in this largely insectivorous species (McLachlan *et al.* 1979; A.A. Crowe unpubl. data)? To answer this question, I must consider the White-fronted Sandplover breeding and environmental data collected at Ouskip.

Reproductive success is dependent on the synchronization of the physiological mechanisms which control reproduction with some environmental cue(s), which ensure the maximal survival of both the parents and their offspring (Immelmann 1971; Lofts & Murton 1973). Jones & Ward (1976) have shown that one of the proximate factors which influence the timing of reproductive

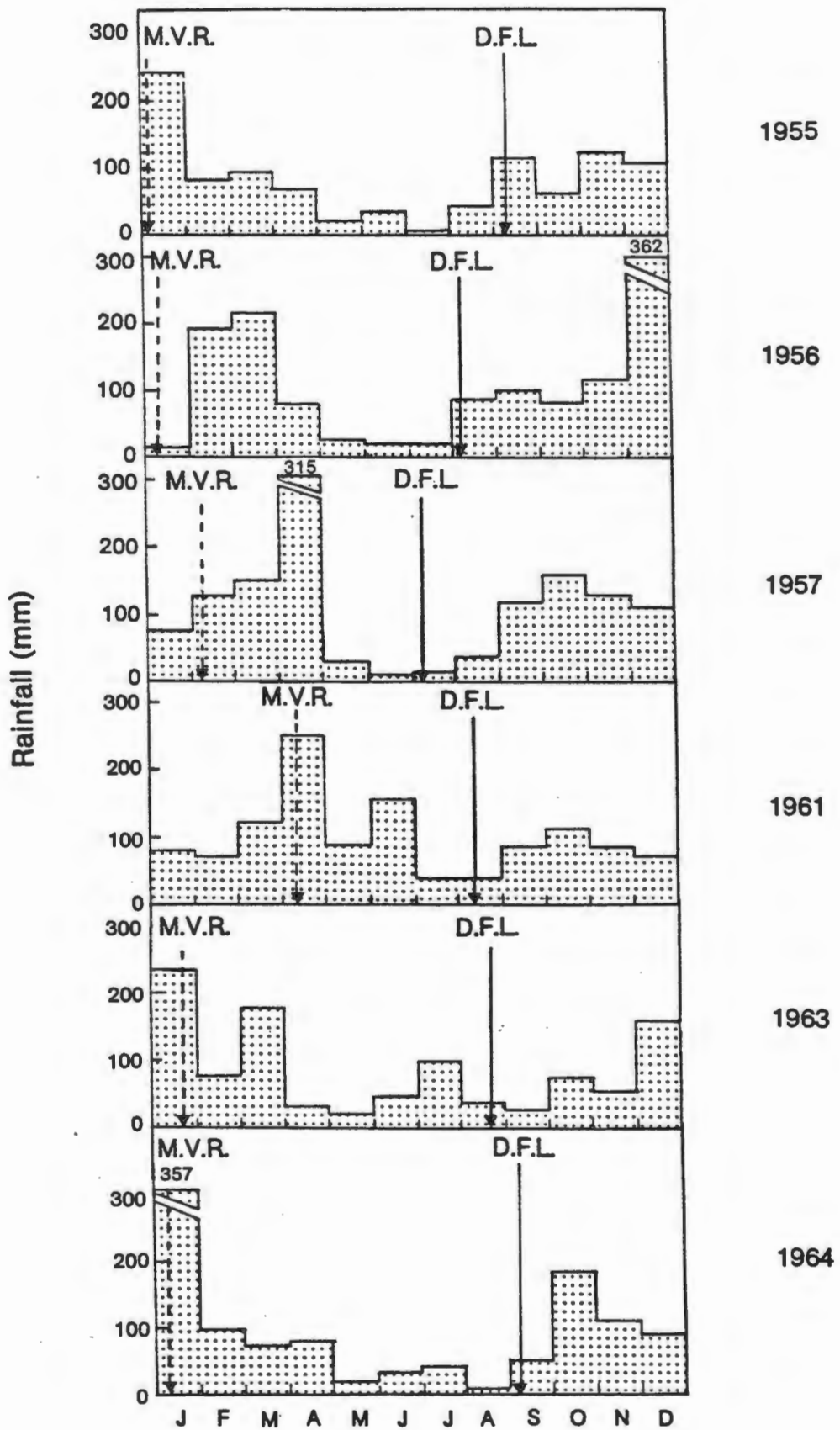


FIGURE 5.4

Temporal variation in: modal day of first laid egg (D.F.L.), modal vector of rainfall (M.V.R.) and distribution of rainfall at unit 12

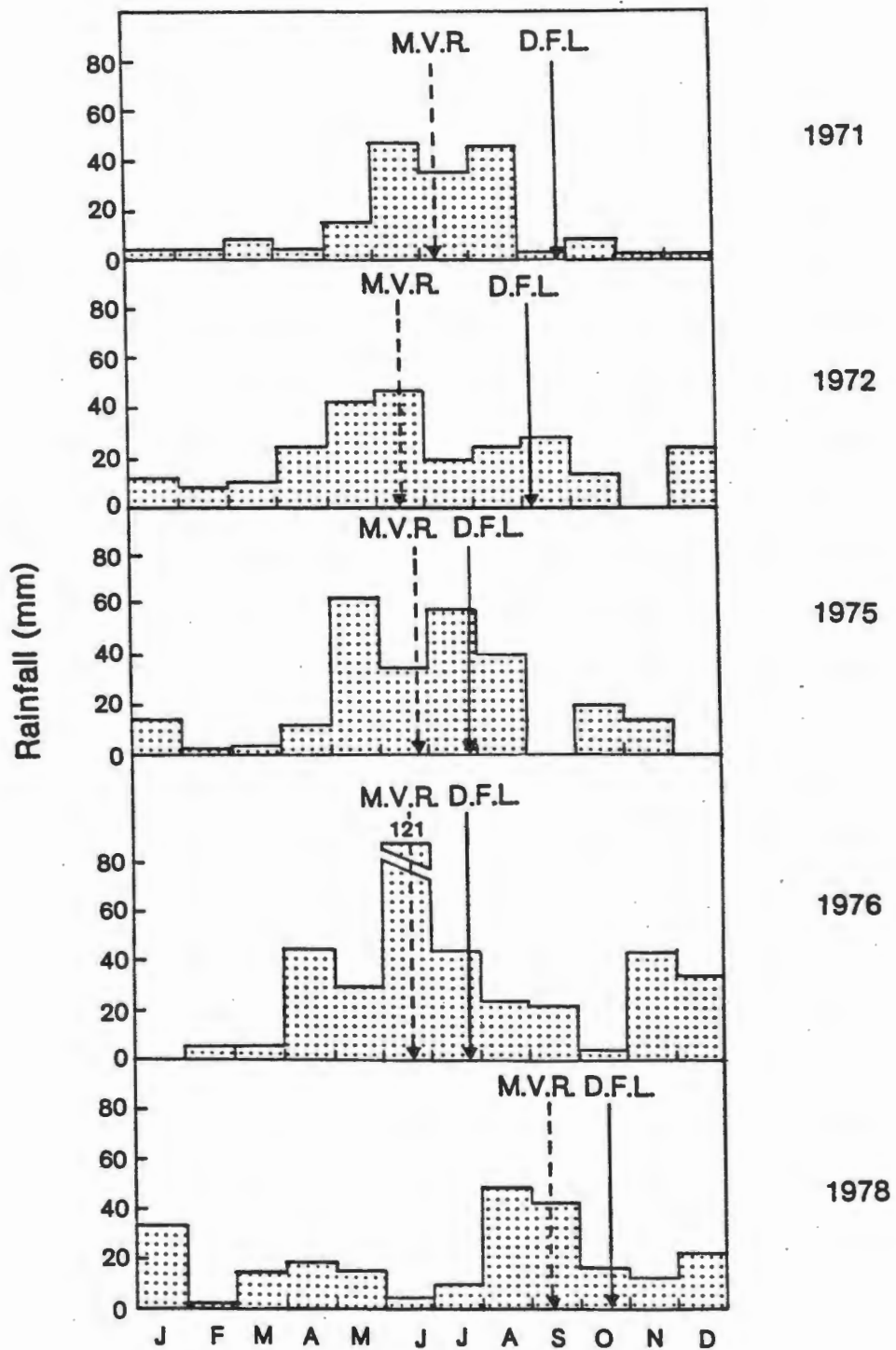


FIGURE 5.5

Temporal variation in: modal day of first laid egg (D.F.L.), modal vector of rainfall (M.V.R.) and distribution of rainfall at unit 4

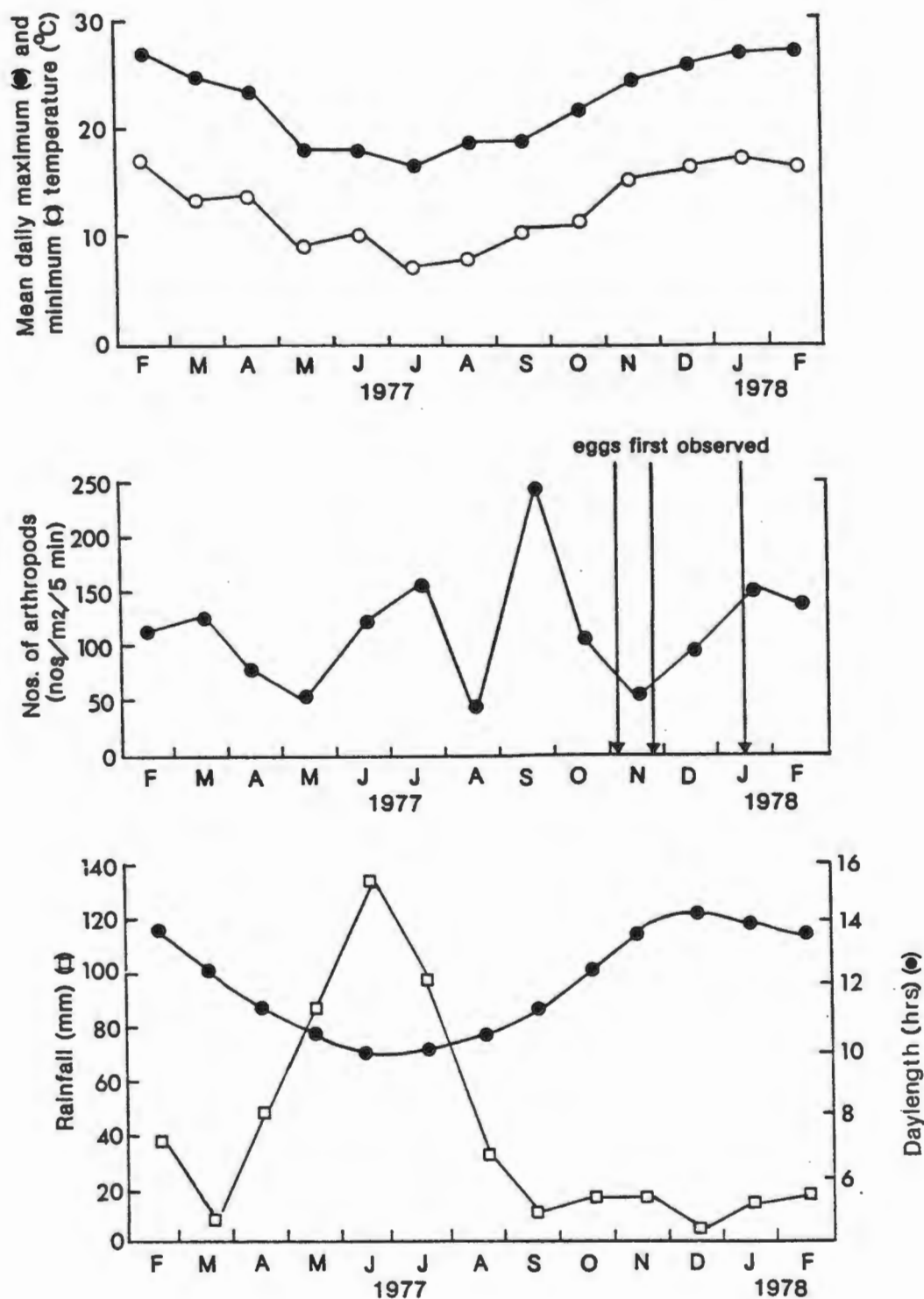


FIGURE 5.6

Date on which eggs were first observed, and monthly variation in temperature, rainfall, daylength and potential invertebrate prey at Ouskip, Cape

activity in birds is a food supply which can satisfy the protein requirements of the laying female. Ricklefs (1974) calculated that the daily energy requirement of egg laying in shorebirds was 149% basal metabolic rate (BMR), while in passerine birds it was only 45% BMR. King (1973) estimated that daily egg laying in free-living birds would require a net increase of 22-44% in daily energy requirements in shorebirds. The White-fronted Sandplover egg, at approximately 25% of total body mass, is relatively large for a member of its family (Lack 1968). Egg production must therefore impose a high energetic cost to the laying female White-fronted Sandplover. Thus, there must not only be an ample food source to replenish her energy losses due to laying, but there must also be an adequate food supply within the territory for the precocial chick. The breeding birds observed at Ouskip during 1977 and 1978, laid their eggs after a peak in the abundance of food (Fig. 5.6). Assuming that all eggs hatched successfully, the young would have hatched when the food supply was rising once again, and there were in fact more daylight hours in which to forage (Fig. 5.6). Therefore, I believe that the cause-effect relation between rainfall and breeding the White-fronted Sandplover is mediated through the abundance of high quality food. The question may well be asked: why did the birds not lay after the food abundance peak of June and July? The efficient growth of precocial young, especially shorebirds, is impaired at low ambient temperatures, due to their inability to regulate their body temperature (Ricklefs 1974). This would put a premium on producing young at times when the ambient temperature was suitable and when food was readily available. Had the Ouskip White-fronted Sandplovers laid in June/July, the young would have hatched in July or August, when local ambient temperature is still low (Fig. 5.6).

In southern Africa, White-fronted Sandplovers breed in 'winter' only in Natal, Mocambique, Zimbabwe and Zambia, where conditions are largely tropical. In Zambia and Zimbabwe where the White-fronted Sandplovers nest on river banks, breeding must be timed to occur prior to the onset of the wet season, to avoid the danger of flooding.

The results which I have obtained for White-fronted Sandplover breeding seasons are consistent with those of Moreau (1950), who found that, in Africa, the breeding season of insectivorous land birds shifted from late in the single rainy season in the southwestern Cape to well in advance of it, in the north. Moreau (1950) felt that this geographical variation in breeding season allowed the birds to keep in step with the main flush of vegetation, so that the young would hatch when insects are in abundance. Winterbottom (1963b) found a similar pattern for several small plover species in southern Africa, but offered no explanation for these patterns.

The White-fronted Sandplover in southern Africa exhibits paired, territorial behaviour, throughout the year (W.J. Lawson unpubl. data, A.A. Crowe unpubl. data), and has precocial young. This species also shows a preference for sandy beaches (Maclean 1985; Summers et al. 1976) and sandy river banks (Benson et al. 1971). Southern African sandy beaches are characteristically geologically and biologically unstable (Brown 1964). I suggest that the sustained pair-bond and year-round territoriality in the White-fronted Sandplover are adaptations which allow pairs to breed as soon conditions are suitable. The defended area ensures an adequate food supply for the pair in those months during which food is scarce, and also during the

austral summer when southern African sandy beaches play host to thousands of Sanderlings (Calidris alba). Close pairing allows a relatively quick response to conditions suitable for breeding.

5.5 Summary

Geographical variation, and year-to-year variation within two geographical areas, in the breeding season of the White-fronted Sandplover Charadrius marginatus in southern Africa are analyzed statistically. There is significant geographical variation in breeding season, and year-to-year variation within an area which has winter (May - August) rainfall. There is no year-to-year variation in breeding season within an area with summer rainfall. Both geographical and year-to-year variation in breeding are paralleled by variation in patterns of rainfall. Within winter rainfall areas, breeding follows the wet season, and the mean date of first laid egg was earlier in years during which peak rainfall was also early. In areas with summer rainfall breeding precedes the wet season, and is later when rainfall is also later in the year. The possible cause-effect relationship between rainfall and the breeding periodicity of the White-fronted Sandplover is discussed.

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6. SUMMARY AND SYNTHESIS

The aims outlined in the GENERAL INTRODUCTION are subdivided into a number of points or questions within each chapter, and these are dealt with in detail in the respective chapter summary sections. The Summary (1 - 7 below) is intended to outline the main findings given in these summary sections and the synthesis (8 below) is designed to link them into a cohesive whole.

1. Seasonal changes in the avian population of a southwestern Cape sandy beach

Bird populations and species richness and at Ouskip, a southwestern Cape sandy beach, varied markedly between the austral winter and summer. During the austral summer, migrant shorebirds from the northern hemisphere dominated the avian population numerically and in terms of energy requirements, and there were five species seen on the beach. Sanderlings Calidris alba (the dominant migrant numerically) and White-fronted Sandplovers Charadrius marginatus (a year-round resident) were the two shorebird species most consistently observed in the intertidal area during the summer. During winter, only two species, White-fronted Sandplovers and Kelp Gulls Larus dominicanus were observed at Ouskip.

Comparison between the sandy beach avian population at Ouskip and those at Port Elizabeth (eastern Cape) and Umdloti (Natal) indicates that the overall energy requirement of the Ouskip avian population is much greater than that of Port Elizabeth which, in turn, is greater than that of Umdloti. I suggest that these marked differences are related not only to variation in the standing crop biomass of invertebrate prey, but also to the predictability of the food sources and the availability of

alternative foraging habitats. The apportionment of the energy requirements between the resident and migrant populations varies between the three areas. The energy requirements of migrants at Ouskip and Umdloti are much greater than those of resident shorebirds, whereas these differences are much less at Port Elizabeth, perhaps due to seasonality of food sources; Port Elizabeth being the least seasonal and Ouskip the most seasonal.

2. Systematics and global distribution of White-fronted Sandplovers and Sanderlings

Of the two most frequently observed small shorebird species on the Ouskip beach, the Sanderling is a Holarctic migrant and the White-fronted Sandplover a territorial, year-round resident. Sanderlings breed during the boreal summer in the Arctic and tundra regions, north of 73° N latitude. During the boreal winter, they migrate to continental coasts, between 60° N and 60° S latitude, and occur at varying densities. The highest recorded wintering densities of Sanderlings were those recorded during this study in the southwestern Cape. The Kentish or Snowy Plover Charadrius alexandrinus, the Red-capped Plover C. ruficapillus and the White-fronted Sandplover which form the superspecies C. alexandrinus have a wide global distribution, overlapping greatly with the wintering range of Sanderlings. Those subspecies of White-fronted Sandplovers (C. marginatus marginatus, C. m. arenaceus and C. m. mechowi) are found in Africa from approximately 15° N along marine coasts and, to a lesser extent, along the banks of larger rivers. Although there is little information available as to the degree of site tenacity of many of these African populations, the population at Ouskip was resident throughout the period of the present study. In southern

Africa, both White-fronted Sandplovers and Sanderlings are more abundant on western shores which are washed by the cool Benguela Current. Sanderling abundance in the western hemisphere is also greatest in those areas of seasonal upwelling in coastal waters.

3. Morphology

Morphological comparisons between these two small shorebirds indicate that Sanderlings are sexually dimorphic in mensural characters, and that White-fronted Sandplovers are not. In Sanderlings, bill length was the most important discriminator of sex. Although White-fronted Sandplovers and Sanderlings are similar in size, in comparison with the other avian species found on sandy shores, Sanderlings are heavier and have longer bills, wings and legs than White-fronted Sandplovers. Sanderlings can therefore potentially obtain prey from deeper in the substratum than White-fronted Sandplovers, and potentially exhibit different spatial and temporal patterns of habitat use.

4. Foraging behaviour

The foraging behaviour of the Sanderling and White-fronted Sandplover at Ouskip differed strikingly. Although both species exhibited a tidal cycle in foraging activities, rather than a diurnal cycle, White-fronted Sandplovers tended to feed during the latter half (i.e. mid to high tide), whereas Sanderlings fed during the first half of the tidal cycle (i.e. low to mid tide). Both species' foraging activity also varied spatially and seasonally. White-fronted Sandplovers fed primarily in drier microhabitats above high tide level, and Sanderlings in wetter microhabitats near the water's edge. Sanderlings spent more time feeding immediately before and after migration. White-fronted Sandplovers increased their feeding time during the

austral winter, when they used a broader range of sandy microhabitats and ephemeral freshwater ponds in the dunes. Each species had characteristic foraging methods, which are related to its use of different microhabitats and prey. Preliminary data suggest that, when conditions on the beach are unsuitable, Sanderlings may switch their foraging habitat to freshwater and estuarine coastal water-bodies.

5. Maintenance of inter-specific differences in foraging behaviour

Inter-specific aggression was observed only when there was both spatial and temporal overlap between the species' foraging ranges, and this resulted invariably in Sanderlings being displaced by White-fronted Sandplovers. Intra-specific aggression among Sanderlings was observed only once, during an instance of localized high prey density. White-fronted Sandplovers were territorial throughout the year, and vigorously defended their territories against conspecifics. The divergent foraging behaviour of these species appeared to be unaffected by densities of conspecifics or of other species present on the beach, and cannot be interpreted as evidence for interspecific competition.

6. Flocking in Sanderlings

The frequency distribution of flock sizes of wintering Sanderlings foraging on the sandy beach at Ouskip was bimodal, with a peak at small flock sizes and another at large flock sizes. I hypothesize that large groups of Sanderlings consist of individuals searching for subterranean prey, and small groups consist of subsets of these larger groups which have located food

patches. This hypothesis does not apply to flocks of Sanderlings foraging on visible surface-living prey, since inter-bird distance between flock members increased with the increased use of pecking as a mode of foraging. This increase presumably decreases the interference effects which attend the pecking mode of prey capture of surface dwelling prey. There was no evidence of the influence of any avian predator on Sanderling flocking patterns as has been observed in California.

7. Breeding activity of White-fronted Sandplovers

Analyses of unpublished nest record card data suggest that there is significant geographical variation in the breeding season of the White-fronted Sandplover, and significant year-to-year variation within an area which has winter (May - August) rainfall. There was no year-to-year variation in breeding season within an area with summer (November - February) rainfall. Both geographical and year-to-year variation in breeding are paralleled by variation in patterns of rainfall. Within winter rainfall areas, breeding followed the wet season, and the mean date of first laid egg was earlier in years during which peak rainfall was also early. In areas with summer rainfall, breeding preceded the wet season, and was delayed when rainfall was also later in the year. The possible cause-effect relationship between rainfall and the breeding periodicity of the White-Sandplover is the strong positive effect that rainfall has on the amount and availability of high quality arthropod food. Since breeding in White-fronted Sandplovers in the southwestern Cape occurred during the austral summer, when they are vastly outnumbered by Holarctic migrant shorebirds, it is concluded that migrants do not have an important effect on breeding activities of these residents.

8. Synthesis

The results of this study, and published information for Sanderlings on their breeding grounds, are summarized as an annual cycle in Fig. 6.1. During the austral summer, Sanderlings at Ouskip make use of resources which are not exploited by the resident White-fronted Sandplovers. During the austral winter Sanderlings migrate to their northern hemisphere breeding grounds, where they encounter an enormous food supply, higher ambient temperatures and longer days. It is only during this period of the cycle that White-fronted Sandplovers utilize resources which are normally used by Sanderlings. The factors which are controlling these species locally appear to be important factors which shape the annual cycle of these two species throughout their distributional ranges. In the case of the resident White-fronted Sandplover, behavioural patterns, and ultimately population regulation, "is probably a dynamic relationship involving the entire year" (Cox 1985). For Sanderlings the results of this study combined with information from their breeding grounds, support Schneider's (1981) hypothesis that shorebird migration is driven by global patterns in food availability. Variation in activities of these species appear to be synchronized with prevailing environmental conditions, and by each species' physiological needs, rather than by the presence or absence of each species. Therefore, although competition might have played an important role in the evolution of activity patterns of White-fronted Sandplovers and Sanderlings in the past, it does not appear to be playing a significant role at present.

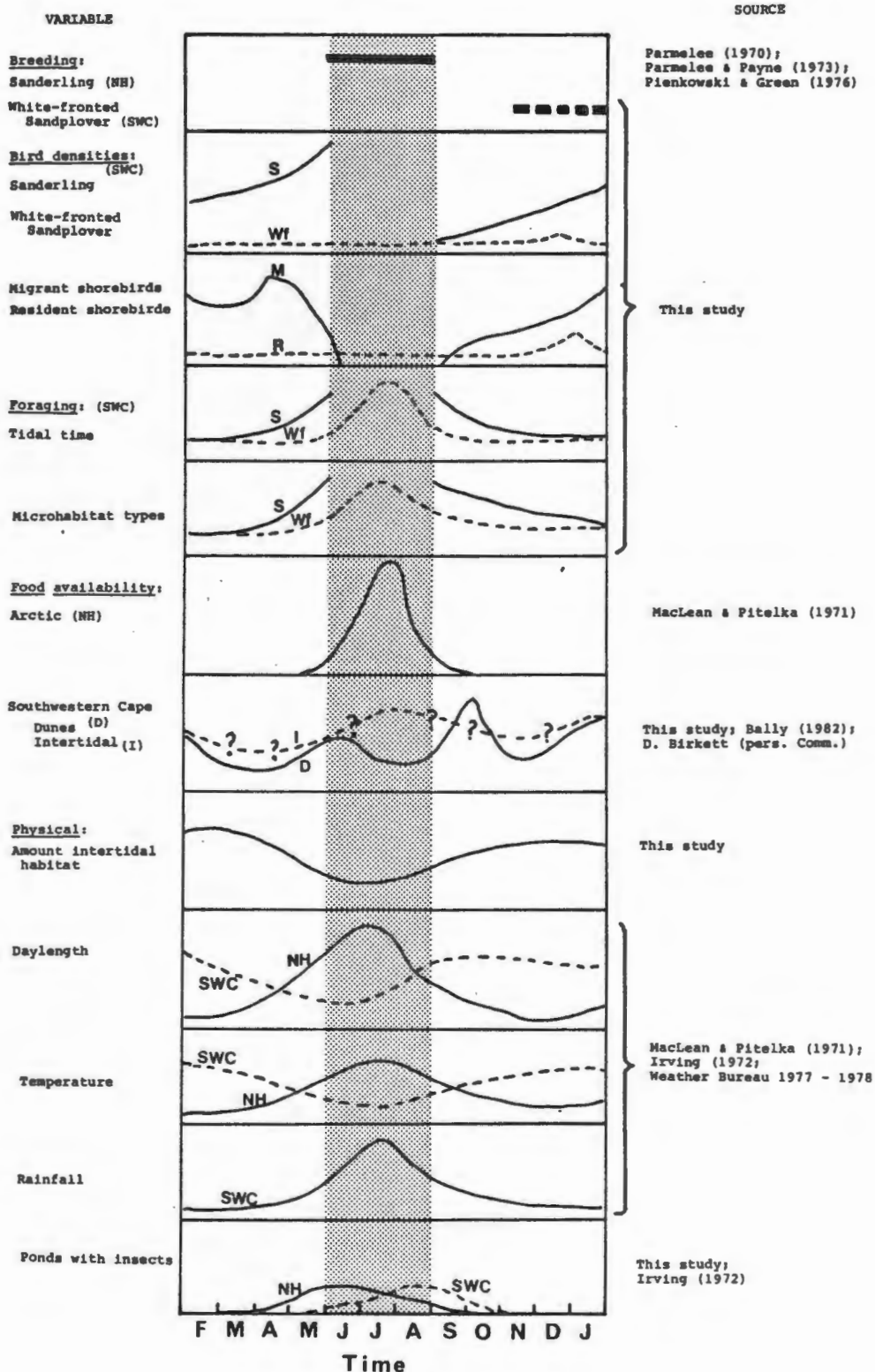


FIGURE 6.1

A summary of variation in the activities of White-fronted Sandpipers (Wf) and Sanderlings (S), in relation to environmental conditions at Ouskip and on Sanderling breeding grounds. SWC = southwestern Cape; NH = northern hemisphere. Shaded area indicates austral winter/boreal summer. (Y-axes are not to scale)

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