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ANNOUNCEMENTS

Shorebird Symposium

The North American Section of the Wader Study Group hopes to hold a 2-3 day Symposium on the biology and conservation of shorebirds in 1982 (spring or fall) in the Washington, D.C., area. The decision to proceed with arrangements will depend on a sufficiently strong expression of interest by biologists and other interested parties. If you are interested in such a meeting and would probably be able to participate or attend, please contact Marshall A. Howe, Migratory Bird and Habitat Research Laboratory, Laurel, Maryland 20811, U.S.A. (301)-776-4880, as soon as possible.

A.O.U. Brewster Memorial Award

At its meeting in Fort Collins, Colorado, in August 1980, the American Ornithologists' Union presented Frank A. Pitelka with the Brewster Memorial Award for 1980 for his work on arctic ecology and studies of shorebirds.

Colour-marking and surveys

Members are referred to the last Bulletin, No. 29, August 1980, for announcements concerning current colour-marking and survey schemes involving shorebirds. Anyone wishing to have announcements made for such projects should contact the Editor.

SANDERLINGS *Calidris alba* AT BODEGA BAY: FACTS, INFERENCES AND SHAMELESS SPECULATIONS

by J.P. Myers

In the winter around Bodega Bay, California, Sanderlings *Calidris alba* vary their spacing behaviour from persistent territorial defence to tight flocking. At times, the entire length of Salmon Creek Beach (Figure 1) is occupied by 100 or more territorial birds, each defending its own 40+ m of sandy beach. Yet at other times there is no sign of territoriality throughout the Bodega Bay area. Since 1974 our research group at the Bodega Marine Laboratory has studied the ecological and behavioural bases of this variability (see Myers et al. 1979a,b, 1980a, Connors et al. 1981). Our goal, ultimately, is to unravel the ecological factors promoting such remarkable behavioural diversity. At the same time, we are concerned with building a solid empirical appreciation for the ecology of waders on their wintering ground - both in relation to how this figures in population regulation and to the evolution of species' adaptations. Our focus has led us, necessarily, beyond the immediate territoriality/flocking issue to questions concerning Sanderling movements within and away from the Bodega Bay area, foraging tactics, and flock cohesiveness, as well as studies on prey availability and energetics.

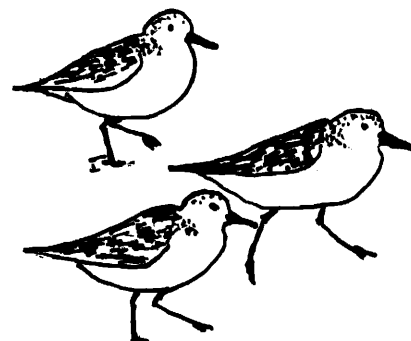
I shall discuss these topics here in smorgasbord style, outlining for each question where our research is going and why it has taken that course. My intent is neither to present a final, definitive summary nor to duplicate material that we have already published. I hope instead to infuse the discussion with a considerable measure of speculation.

Background: annual cycle and survivorship

Sanderlings inhabit the Bodega Bay area from July to May, but are most common between September and April (Figure 2). Members of the local wintering population begin to reappear during the last two weeks of July. We know this because among the earliest arrivals are birds colour-ringed at Bodega Bay during prior years, individuals that remain in the area for the duration of the season.

The juvenile influx peaks during mid and late September, by which time much of the adult population has returned. Juveniles rarely appear before the end of August. As with the adults, among the first of the arriving juveniles are birds that will remain at Bodega Bay for the rest of the year (based on colour-ringing). In neither age class do we see an indication of a large fall transient population.

The combined forces of adults and juveniles push the local Sanderling population to between 500 and 700 birds by early October (Fig. 2). This total remains relatively stable through fall and early winter, but begins to decline by February. In midwinter this represents approximately 25% of the Sanderlings wintering on 55 km of beach



scattered over 90 total km between Jenner and the mouth of San Francisco Bay (Figure 3). The population at Bodega Bay drops sharply in late March and April (Fig. 2). Small flocks including locally ringed birds remain on the beaches until late May and during this month transients stop off briefly and in low numbers. The Bodega Bay estuary-beach system does not appear to be a staging area for Sanderlings moving north along the west coast of the U.S.

A high proportion of birds ringed at Bodega Bay return in the subsequent year. Based on returns between 1976 and 1978, calculated only for individuals ringed freshly the previous year, we observe return rates of 72% for adults versus 50% for first-winter birds. These rates differ significantly ($\chi^2=11.4$, $P < .001$; Table 1). Birds ringed more than 1 year before are excluded because ring loss was noticeable after 2 years (using A.C. Hughes split rings).

These return rates are higher than expected: Boyd (1962) estimated that Sanderling adult and first-year annual survivorship was 56% and 38%, respectively, for passage migrants through Norway. Many factors, including geographic variation or methodological bias, could contribute to these differences. It should be noticed that the differences between our estimates are conservative since at Bodega Bay we measure return rate rather than survivorship.

We found no difference in return rate between birds that defended a territory at least once during a given year and those that never defended ($\chi^2=1.95$, $P > 0.16$; Table 2). The sample for this test is small and weakened by the fact that the territorial birds also behaved non-territorially at times (Myers et al. 1979a).

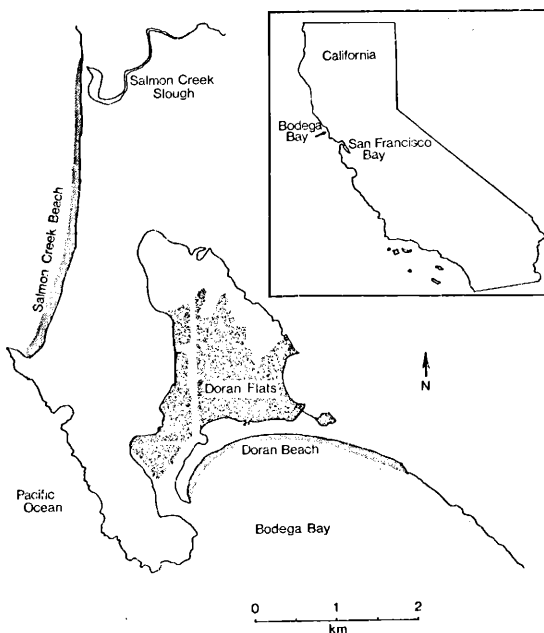


Figure 1. Bodega Bay, California, with inset showing the location of Bodega Bay within California.

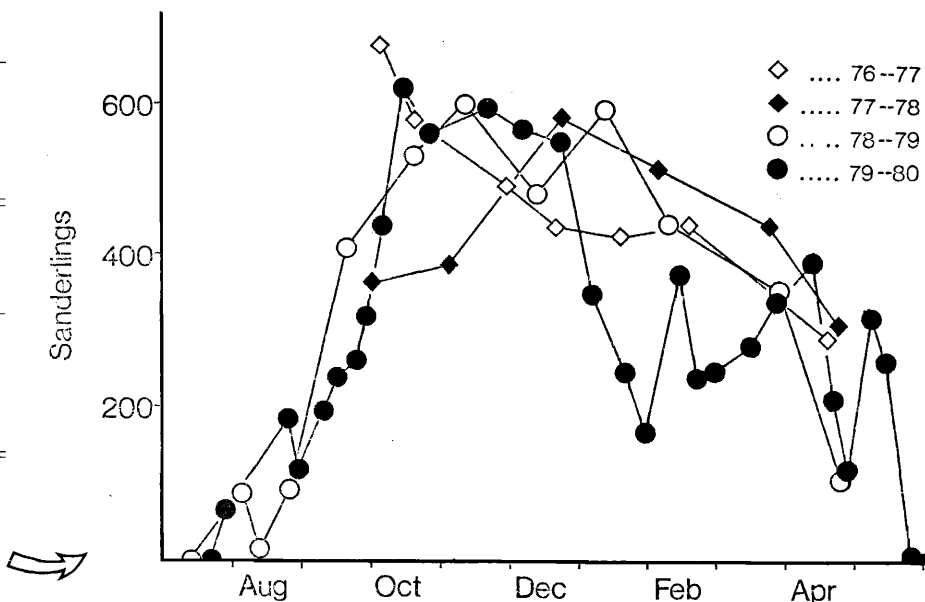
Table 1. Adult versus First-year return rates

| | return | not return |
|------------|--------|------------|
| Adults | 89 | 35 |
| First-year | 52 | 52 |

Table 2. Territorial versus non-territorial return rates

| | return | not return |
|-----------------|--------|------------|
| Territorial | 23 | 8 |
| Non-territorial | 105 | 67 |

Figure 2. Changes in abundance of Sanderling during 4 successive winters at Bodega Bay, California.



Inter-estuarine movements: are Sanderlings opportunistic or site-faithful?

Once back in autumn, individually colour-marked Sanderlings are seen repeatedly in our area throughout the winter. Combined with data showing a usually stable population size through mid-winter (Figure 2), this pattern indicates a relatively conservative life-style for wintering Sanderlings: strong site-faithfulness and a sedentary winter population.

This conclusion would have important implications for coastal management schemes. It suggests that Sanderlings along the California coastline belong to a series of independent wintering populations, sensitive to local resource conditions but immune to events outside their own restricted domain. At the same time, this population structure has more basic biological significance, in that it bears on the likelihood of adaptations to local conditions and on the general issue of opportunistic versus conservative resource-exploitation patterns (see Pitelka et al. 1974, Wiens 1979). With an eye toward these issues, we began to look at Sanderling inter-estuarine movements last year. The results to date indicate a more complex and seasonally varying story than we had anticipated.

During late fall and early winter, the Bodega Bay population was sedentary. But both before mid October and once again beginning in February, individuals moved frequently in and out of the Bodega Bay system. Occurring at separate times of the year and under different resource conditions, we suspect nevertheless that the patterns of enhanced vagility observed in these two periods are functionally related.

As adults return in late summer and early fall, colour-ringed Sanderlings repeatedly move away from Bodega Bay, at least as far as 20 to 35 km to the beaches and lagoons on Point Reyes (Figure 3). Of 71 colour-marked birds that returned to the region by mid October 1979, 16 were seen on Point Reyes at least once: two were seen only at Point Reyes while 14 were recorded both at Point Reyes and Bodega Bay. Of these 14, three were spotted first at Bodega Bay and then again at Point Reyes before returning to Bodega Bay. This same pattern is recurring in Fall 1980. In November and December 1979 the sightings of ringed birds away from Bodega Bay decreased markedly (Fig. 3).

I find this puzzling. The data indicate that in early autumn a sizable fraction of the Bodega Bay population (23% of ringed birds) wanders broadly within a coastal sector of some 40 km but as winter approaches they increasingly restrict their activities to the Bodega Bay system. The wandering does not involve a mass exodus from Bodega Bay, because as some leave others arrive; still others, moreover, arrive and stay without wandering. More peculiar still, Bodega birds (those ringed at Bodega Bay in prior years) ultimately return in late fall to Bodega Bay despite their wandering.

Their early fall wandering cannot result simply from migration errors: some return to Bodega Bay and only afterward appear in other areas. It also cannot be a case of sampling alternative sites while choosing a final wintering ground. Were this the case I would expect a more diffuse pattern to which the banded population re-sorted throughout the region each fall. Neither is moulting the answer: many birds remain at Bodega Bay throughout their fall moult.

I suspect that fall wandering by Sanderlings may relate to their use of localised and temporary resource hot spots on a regional scale. This would lead to the observed pattern if the abundance, predictability, and stability of these hot spots undergoes some seasonal change. Sanderlings' use of beach wrack, an abundant but regionally patchy and somewhat unpredictable fall resource (Yaninek 1979), is consistent with this interpretation.

Sanderlings also wander regionally later in the season during some years. Beginning in late December 1979 and continuing through February 1980 a series of storms beset Bodega Bay. Sanderling numbers plummeted (Fig. 2), no doubt in response to deteriorating food conditions caused by beach storm erosion. The decline, however, was not just a mass exodus. Instead, it also involved greatly increased turnovers of individuals: up to 50% of the marked birds present at Bodega Bay changed from one week to the next. Searches in surrounding areas revealed that they began to use other feeding sites away from our locale, but that at the same time, individuals returned regularly to our beaches. The scale and frequency of these movements evoked images of a seething mass of Sanderlings in turmoil along the coast. We began to have sightings of marked birds reported from beaches up to 200 km away.

The most dramatic example of this turmoil began when Abbott's Lagoon on Point Reyes (Fig. 3) opened to the sea for the first time in over five years on 7 March 1980, exposing several hundred metres of fresh foraging substrate rich with two amphipods, *Corophium* and *Anisogammarus*. Within four days over 1300 Sanderlings began using the site, one which had been unsuitable for their foraging since the rainy season began in October. Thirty-seven of these were colour-marked birds from Bodega Bay, and of them, several moved back and forth repeatedly, a distance of 23 km.

These observations raise several questions. How did the birds respond so rapidly to the new food resource? If feeding conditions were good, why did some return to Bodega Bay? I suspect the answers are linked to the high turnover rates mentioned above: when resource distributions change rapidly, individuals ought to increase their exploration of alternative feeding sites, in anticipation of and/or in response to a deterioration in local feeding conditions.

Testing these ideas will require more data on turnover rates, on patterns of individual movements, and on temporal patterns in the resource base itself. At the very least, we have learned already that viewing this particular Sanderling population as site-faithful and sedentary oversimplifies their resource exploitation pattern. What is more, I believe that this on-again, off-again opportunism is ultimately responsible for the fact of both territorial and flocking individuals within a local population.

Do Sanderlings forage optimally?

The discussion above poses a series of questions about foraging tactics. How do Sanderlings respond to changes in resource distributions? Do they explore a series of feeding sites even if it means leaving the one that is best at the moment? Do they adjust their behaviour to differences in prey dispersion in order, for example, to use patchily or evenly distributed resources more efficiently? We are studying these and related issues using a combination of field observations and laboratory experiments.

In the field, we are examining Sanderling space-use patterns under conditions of different resource stability. By space-use pattern I mean the size of an area an individual uses and the distribution of its activity within that area - unimodal, bimodal, toroid, etc.

The bird data come from repeated mappings of the positions of colour-marked individuals along Salmon Creek Beach (Fig. 1). For a week at a time, a team censuses the length of the beach once per hour throughout the mid to high portions of the tide cycle, when Sanderlings are on the beach (Connors et al. 1981). From these data we obtain an estimate of the size and shape of the home range of the 'average' Sanderling along the beach during that week. This analysis depends upon a computer simulation technique developed by Ford and Krumme (1979) and I leave the technical explanation to them.

Figure 4 presents three typical results from this analysis. Each graph shows the average Sanderling home range on Salmon Creek Beach during one sampling period as a probability distribution function. The height of the function indicates the probability of occurrence of the average Sanderling within a particular segment of its home range. It is important to bear two points in mind: first, this home range estimate is for the beach only. Sanderlings move between the beach and nearby sandflats on a regular tidal schedule (Connors et al. 1981); their use of the sandflats is not included in this analysis. Second, the abscissa in Figure 4 does not refer to a particular location on a real beach, but rather to a position along an abstract beach over which the average Sanderling moves. Thus on Salmon Creek Beach in November 1979 we did not have a single concentration of birds between 1600 and 2400. Instead, the graph indicates that the average Sanderling during this period restricted most of its activity to a 800 m stretch of beach, that it moved broadly and evenly within that region, and that it occurred at a low probability along 4 km of beach. In February 1980 Sanderlings

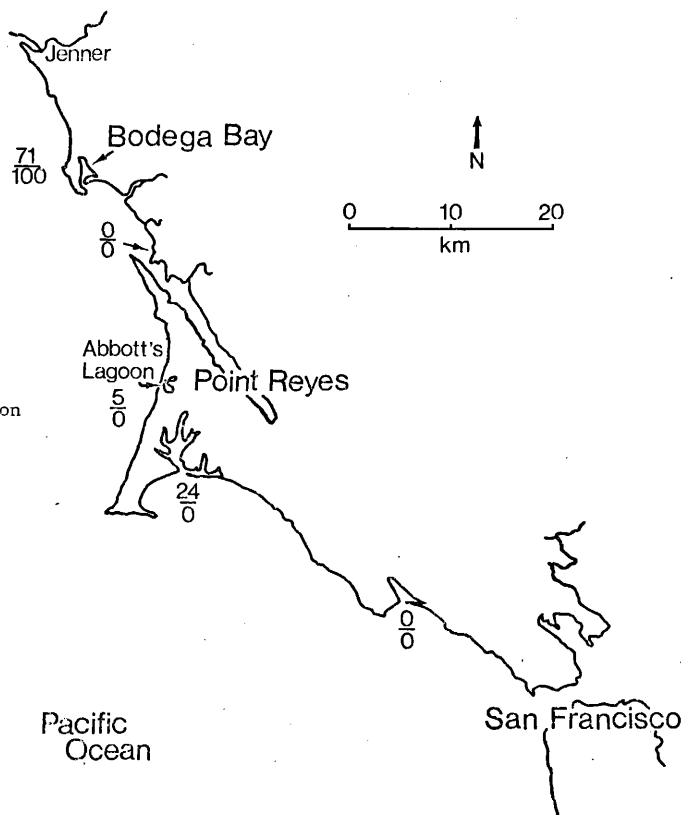


Figure 3. Geography of Bodega Bay-Point Reyes region and distribution of ringed Sanderlings observed during censuses. Numbers along coast indicate percent of total ringed individuals located during two different censuses at a given site: numerator, percent of 42 total seen on 27 September 1979; denominator, percent of 124 total seen on 15 November 1979.

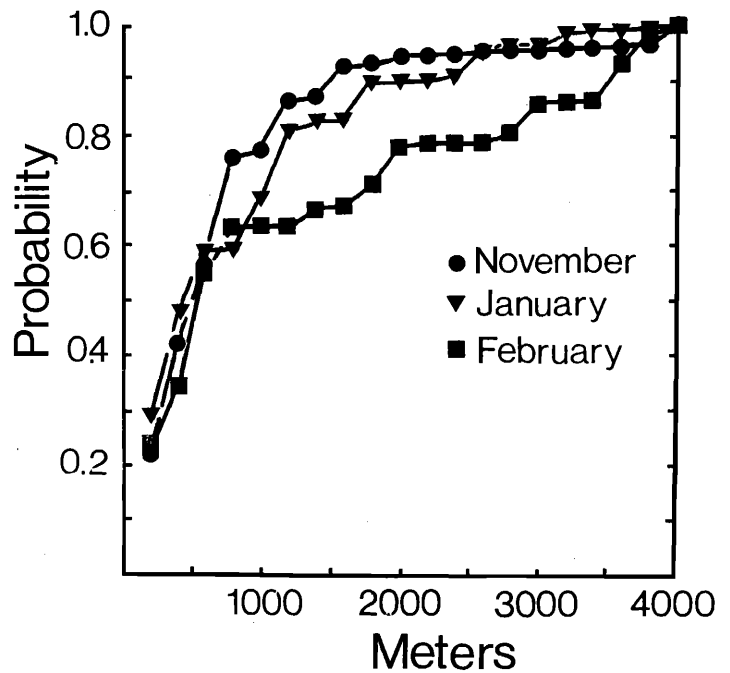
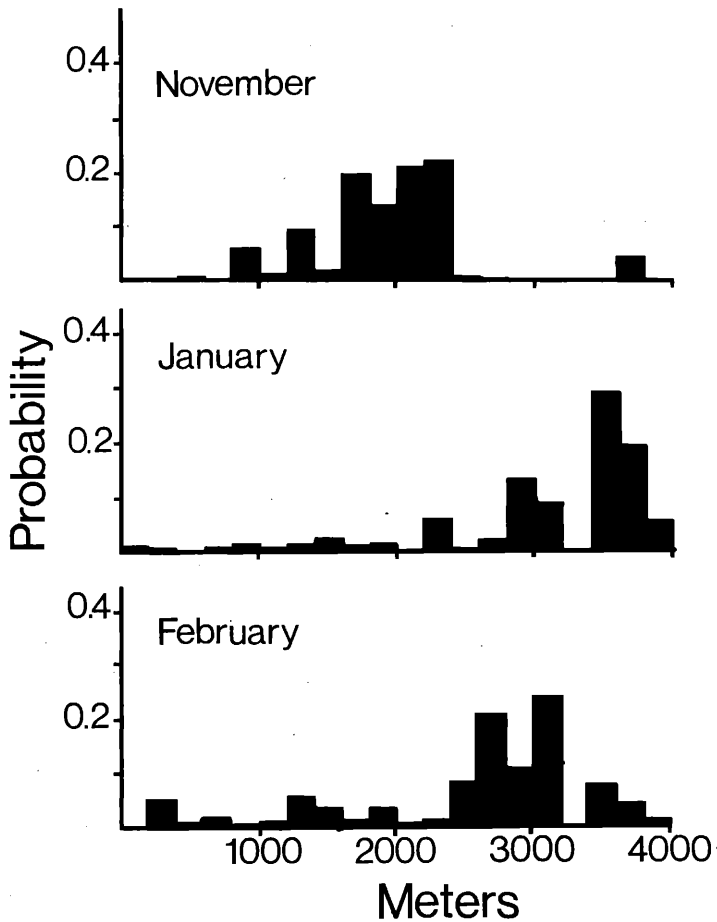


Figure 5. Cumulative probability distribution function of Sanderling activity as a function of beach segment length. See text.

Figure 4. Sanderling average home range during 1 week sampling periods in three months of 1979-80 winter. Height indicates probability of finding average individual within a given region of its home range. Calculated through computer simulation following Ford and Krumme (1979). See text.

had a more diffuse space-use pattern, with the activity centre again roughly 800 m long but with more activity away from this region, distributed in several small, peripheral modes.

Figure 5 brings out an important contrast between these space-use patterns, showing for each period the cumulative proportion of a bird's activity occurring within a given length of beach. During each of the months shown, approximately 60% of a bird's activity is confined to 600 m of beach. For November and January, 80% occurs within 1200 m and 90% within roughly 2000 m. In February, by contrast, the 80% level is not reached until 2800 m and the 90% until 3600 m. Clearly Sanderlings moved far more broadly during the latter period.

But our sampling must continue. As might be predicted, a simple theoretical framework based on foraging considerations alone does not do justice to the revealed complexity of beaches, Sanderlings, and Sanderling predators. It appears now that the multi-modal character of Sanderling space-use patterns increases through the winter, but whether that is due to their responses to changes in resource stability, to changes in prey patchiness and abundance over space, or to variations in disturbances by predators is not yet clear.

In the laboratory, we have run a series of experiments on foraging tactics. One set, now completed, asks whether individuals adjust their foraging behaviour to different prey dispersions: does a bird that has been trained on patchy prey forage differently than one on even prey? A second set, anticipated for this coming winter, will test whether an individual attempts to maximize its intake rate by finding the best site or whether it merely attempts to satisfy some threshold intake rate requirement. These experiments follow some of the protocols outlined in a previous WSG Bulletin note on prey availability (Myers et al. 1979c, 1980b).

Winter territories: when and where to defend?

Our previous work suggested that Sanderling territorial defence is more likely in areas of intermediate prey density (Myers et al. 1979b). Where prey are sparse, not only are Sanderlings non-territorial - they usually are absent. But when prey are very abundant territoriality is also rare, despite the fact that Sanderlings may be common. This resembles patterns seen in other birds defending feeding territories (Myers et al. 1980a).

We have continued to study the relationship between territoriality and food density and in particular the reasons why territoriality ceases at high density. Our data to substantiate an 'upper threshold' for defence have grown substantially (Figure 6). But our attempts to test different hypotheses for this threshold (see Myers et al. 1980a) have been stymied by an unexpected twist, namely the disappearance of territorial behaviour in our wintering population. During each of the last two winters we have detected fewer than five individuals along Bodega Bay beaches showing signs of defence. Defence has been so unusual that none of the 600 transects sampled during these winters have crossed defended areas (Fig. 6, lower histogram; this figure summarizes data for 1978-79, and the results for 1979-80 are identical). Because prey densities in the last two winters have been within the range of densities defended previously (Fig. 6, compare upper and lower histograms), we believe that resource conditions are not the key to this gross change in Sanderling behaviour.

The likely cause involves one or more Merlin *Falco columbarius* that have established winter residency of late at Bodega Bay (Table 3). During our first years of study, Merlins rarely occurred in the area. But during the last two years, not only have observations been common but we have seen Merlin actively defending the beach against other Merlin - a new trophic level for our study of territoriality.

This new development has frustrated plans for energetic cost-benefit analyses of territoriality, necessary to test ideas about the upper threshold. But at the same time it has raised a slew of new issues and emphasized to us that the ultimate expression of spacing behaviour involves compromises among competing ecological requirements. Thus in this case the energetic benefits of defence apparently do not justify the risks of being alone when a serious predator threatens (see Page and Whitacre 1975, Milinski and Heller 1978, Myers 1980). This does not mean Sanderlings will not ever defend when a Merlin is about. What matters is which threat to their survivorship - starvation or predation - weighs most heavily at the moment.

Table 3. Territorial Sanderlings and Merlin at Bodega Bay, California.

| Winter | Resident Merlin | Territorial Sanderlings |
|---------|-----------------|-------------------------|
| 1974-75 | absent | regular |
| 1975-76 | absent | regular |
| 1976-77 | absent | abundant |
| 1977-78 | absent | abundant |
| 1978-79 | present | absent |
| 1979-80 | present | absent |

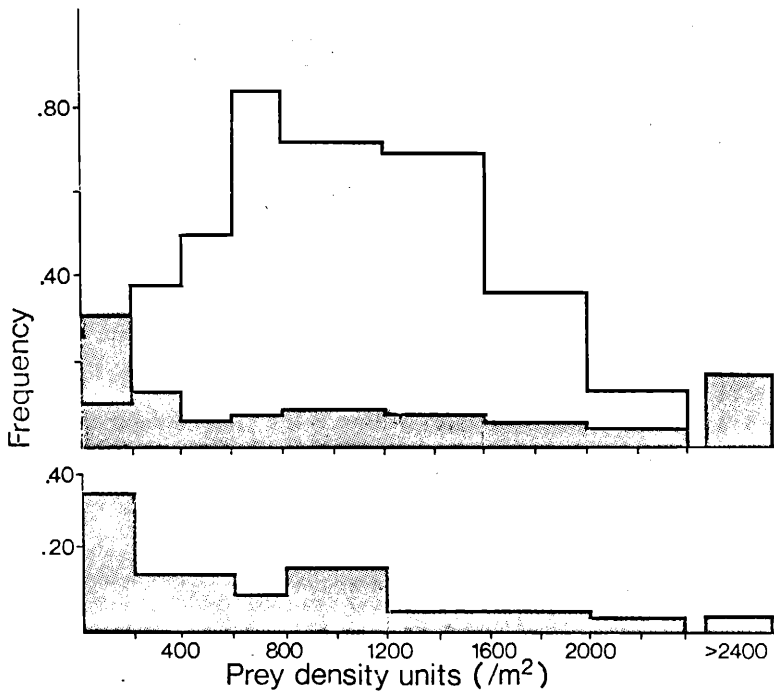


Figure 6. Frequency distributions of prey abundance and territorial defence by Sanderlings in relation to prey density during different raptor conditions. Stippled histogram shows proportion of transects sampled within a given range of prey density (see Myers et al. 1979b, Connors et al. 1981 for prey sampling methods). Clear histogram shows proportion of transects that were on sites defended by Sanderlings. Upper figure: 1979-77 and 1977-78 (no raptor); n of transects = 595. Lower figure: 1978-79 (resident Merlins present, see Table 3); n of transects = 600.

Do Sanderlings have friends?

In interpreting interactions among individuals it is essential to understand their patterns of association. Do they move about in cohesive flocks, interacting with only a select fraction of the local population? Or are groups a random and constantly changing assortment, not allowing for long-term associations between individuals? These patterns set the context for social behaviours and thereby delimit simultaneously both the types of interactions possible and the modes by which natural selection might operate. Long-term associations in cohesive groups set a potential - one not always realized - for complicated interactions dependent upon individual recognition and modified by past histories. They also raise the possibility - again, not a requirement - for kin or group level selection.

Where do Sanderlings fit along this spectrum of flock cohesion? Do individuals in our local population persistently associate with one another? Our data on this come from the same sampling scheme used for studying home ranges along the beach (see above) and therefore the analysis looks only at short-term associations, of one week or less.

To examine the overall patterning of association we have used an index developed by Ekman (1979) in a study of winter parid flocks. His coherence index, C, varies between 0% (two birds are never seen together) and 100% (when one is seen the other is always there).

Figure 7 shows the distribution of coherence values for three different sampling periods during the winter of 1978-79. The average observed values (calculated excluding 0's) are 10%, 10% and 18% for October, January and March, respectively. These averages are quite low compared with the 75% and 79% averages (excluding 0's) reported by Ekman (1979) for Crested Tits *Parus cristatus* and Willow Tits *Parus montanus*, respectively. Neither October nor January differ from distributions generated by random rearrangement of flock composition (expected, Fig. 7; October $\chi^2 = 4.1$, $N_{obs} = 595$, $P > 0.30$; January $\chi^2 = 5.9$, $N_{obs} = 250$, $P > 0.20$).

In contrast, the March observed distribution does differ from random ($\chi^2 = 26.7$, $N_{obs} = 153$, $P < 0.001$). The shapes of the expected distributions change because the underlying flock size distributions change; each random calculation is based on the observed flock size distribution for a given sample.

These results indicate that viewing Sanderling flocks as an anonymous mob may not be far from the truth. Overall, their flock structure is rather loose and associations between individuals do not persist even within the relatively short sampling time (1 week) used for each of these periods. Certainly it is difficult to envision complex behavioural interactions within the flocks based on long histories of interaction or on degrees of relatedness among individuals (see also Owens and Goss-Custard 1975).

The deviation from randomness in March could have resulted from several causes. It could be due to low level but real associations among individuals. Alternatively, it might result from sampling problems: we have only about 20-25% of Salmon Creek Beach Sanderlings marked. Thus, if each bird had a partner (C = 100%), then in only 20-25% of the cases would we detect strong pairs. Finally, the apparent associations between individuals could arise indirectly because different birds feed repeatedly in

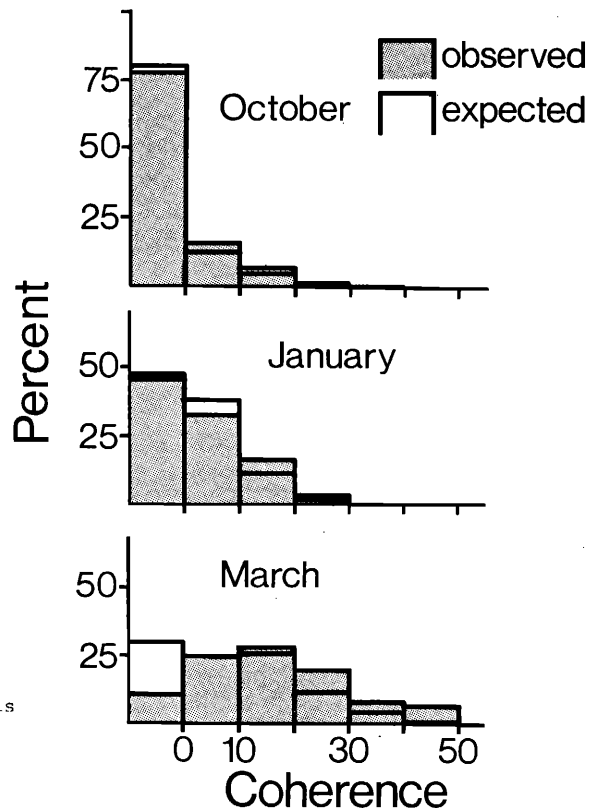


Figure 7. Distributions of observed and expected coherence values for flock compositions observed during three 1-week observation periods in winter of 1978-79. Coherence calculated after Ekman (1979). See text.

the same places. Our goal now is to tease apart these different interpretations. I suspect that the last one is the most accurate.

Prey availability, prey selection, and expected caloric intake rate.

We previously analysed factors affecting prey availability to probing Sanderlings (Myers et al. 1979c, 1980b). This laboratory work yielded a series of regression equations predicting foraging rate from prey density, prey size, prey depth and substrate penetrability. By combining these relationships with field data and with caloric values of different prey sizes and species we can begin to ask how seasonal or spatial changes in prey quality, distribution and abundance affect a Sanderling's caloric intake rate.

Our preliminary analyses highlight a number of important issues in wader ecology, three of which I mention here. First, comparing expected caloric intake rates (calories per second) for a Sanderling foraging on our study plots on the sandflats of Bodega Harbour we observe as much as a 75% decrease from August through December. This change parallels seasonal patterns seen in invertebrate densities reported by Schneider (1978) and Evans et al. (1979). Whether this decrease drops the rate so low that Sanderlings face an energy shortage in mid winter is not yet clear, but the potential is there.

Second, while the intake rate decreased, total prey density at some sampling sites actually increased. This discrepancy was due largely to the confounding variable of size: total prey included all animals retained by a 1 mm sieve. The smaller sizes within this set increased numerically but not enough to offset the effect of disappearing larger size classes.

Third, the calculations suggested that Sanderlings should be highly selective in diet during August but less so in December. This prediction resulted because of the effects of handling time on expected caloric intake rate. Essentially, a bird would waste time if it bothered to handle calorically-trivial prey. By our preliminary calculations, in August a Sanderling can achieve its highest intake rate by ignoring all but the single best prey species (best as determined by calculating intake rate for all different prey species, assuming monophagy in each calculation). Adding more species to the diet actually decreased the expected intake rate even though it increased total prey density. By December this prediction changed because of the decreased abundance of large prey.

Conclusions

Research on Sanderlings at Bodega Bay has led us along a number of ecological trails. How successfully we will unravel the question that brought us here in the first place - territoriality versus flocking - remains to be seen. On the one hand, its resolution has been made more difficult by the local disappearance of territories (see above). But even if initially vexing and unwelcome, this development may prove beneficial in the long run because it has brought out compromise as a central theme in Sanderling ecology. I suspect that compromises pervade Sanderling behaviour, from tactical decisions of patch use while foraging, to patterns of opportunism and site-faithfulness, to determining the risks and rewards of territorial defence.

Determining the rules that shape how Sanderlings balance their competing ecological requirements thus becomes an increasingly important part of our research. Are their behaviours finely tuned, optimal responses to these simultaneous problems? That is what the current drift of behavioural ecology would predict and I find it theoretically appealing. On the other hand, my intuition on this is shaped strongly by long hours of field observation: I suspect their behaviour is ridden with traditions, far from an instantaneous optimum, and that much of the time they drift through routines that meet each requirement but optimize none. The challenge is to reconcile our expectations of how natural selection ought to work with the nitty-gritty of Sanderling behaviour.

Acknowledgements

Research on Sanderlings at Bodega Bay has been a collaborative effort involving many people. Peter Connors first noticed territorial behaviour in Sanderlings at Bodega Bay in 1973; he began the program then and has been involved centrally ever since. Frank Pitelka has provided invaluable guidance and encouragement throughout. R.G. Ford pushed and pulled on ideas about optimal foraging and space-use. Our sampling programs have depended upon armies of observers and invertebrate counters. Chief among these are S.E. Smith, S.L. Williams, B.J. McCaffery, B.B. Smith, C.S.W. Connors, J.S. Yaninek, M. Pritchard and W.D. Shuford. This work has been supported by NSF grants to F.A. Pitelka, an NSF predoctoral fellowship to the author, and funds from the Bodega Marine Sciences Association and the Committee for Afternoon Projects.

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BREEDING SCHEDULE, CLUTCH SIZE AND EGG SIZE OF AMERICAN OYSTERCATCHERS (*Haematopus palliatus*) IN VIRGINIA

by Allan J. Baker and Michael Cadman

Despite extensive studies of the breeding biology of other species of oystercatchers in various parts of the world (e.g. Hall 1959, Harris 1967, 1969, 1970, Hartwick 1974, Heppleston 1972, Summers and Cooper 1977, Webster 1941), the American Oystercatcher *Haematopus palliatus* remains relatively unknown. Over the past three years we have been carrying out studies aimed at providing basic data on the breeding and feeding ecology of *H. palliatus*. Herein we present a preliminary report on some aspects of the breeding biology of the American Oystercatcher at our study site on Wallops and Assawoman islands, Virginia. A more comprehensive paper is currently being prepared for publication elsewhere.

Breeding schedule

During the winter, oystercatchers on the eastern shore of Virginia often congregate in feeding flocks on commercial beds of intertidal oysters. Birds disperse from the winter flocks in the last week of February and the first week of March. In our study area we first observed piping in defense of territory in the last week of February. Most birds arrive at the breeding sites (see Cadman 1979 for map of territories) through the month of March, including migrants which presumably have wintered further south.

In most cases, females arrive on their territories of the previous year before their mates, sometimes as much as three weeks earlier. This is in marked contrast to *H. ostralegus* on Skokholm, for example, where both sexes arrive together (Harris 1967). Lone birds defend their territories until their mates return or until they pair with new mates. Territory and pair-bond fidelity is high and nest scrapes are often placed within a few metres of those of previous years.

Egg-laying commences in early April with a peak in the third week of April. Many early clutches are destroyed by storms and high tides in late April, and this leads to another peak of laying in the second week of May. Hatching commences in mid May with a peak in early June. Egg and chick mortality were so high in 1978 and 1979 that we have few data on fledging; some chicks were flying by mid July. One pair was still together with two begging offspring in early December, but by January all birds rejoin the winter feeding flocks.

Clutch size

Clutches range in size from 1 to 4 eggs, the modal number being 3 (Table 1). When clutches are lost they are usually replaced within two weeks. One female laid three repeat clutches in response to repeated egg predation by foxes. Based on the small samples we have so far obtained, repeat clutches are not significantly smaller than first clutches (Table 1).

Table 1. Clutch size of American Oystercatchers in Virginia

| | N | Clutch size | | | | X |
|------------------------|----|-------------|--------|--------|--------|------|
| | | 1 egg | 2 eggs | 3 eggs | 4 eggs | |
| Overall (1978-80) | 88 | 4 | 33 | 50 | 1 | 2.54 |
| First clutches (1979) | 34 | 1 | 14 | 18 | 1 | 2.56 |
| Second clutches (1979) | 8 | 1 | 3 | 4 | 0 | 2.38 |

Table 2. Size of eggs from complete clutches of American Oystercatchers in Virginia

| | Egg size | | |
|------|------------|-------------|---|
| | Length (L) | Breadth (B) | Volume (L.B ² /10 ³) |
| Mean | 56.8 mm | 39.7 mm | 89.7 cc |
| S.D. | 1.86 | 1.10 | 4.97 |
| N | 89 | 89 | 89 |

Egg size

Descriptive statistics for egg measurements and 'volume' (L.B²/10³) are given in Table 2. The length and breadth of eggs are negatively correlated (r = -0.307, p = 0.003, see Figure 1), reflecting the tendency for long eggs to be narrow and vice versa. Analysis of variance revealed that variation among females in egg size is highly significant (for length F = 1.81, p < 0.05; for breadth F = 6.44, p < 0.001; for volume F = 5.75, p < 0.001). However, unlike some other shorebirds (see Väisänen 1972, Miller 1979), average egg size is not significantly related to female size (as judged by bill length).

H. palliatus resembles *H. ostralegus* in that both species are relatively r-selected, having higher mean clutch sizes and smaller eggs than K-selected species such as *H. fuliginosus*, *H. ater* and *H. moquini*. The latter group of species has modal clutches of two large eggs. Undoubtedly, this dichotomy of investment strategies underscores differences in parental care among oystercatcher species.

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