

# TERRITORY SIZE IN WINTERING SANDERLINGS: THE EFFECTS OF PREY ABUNDANCE AND INTRUDER DENSITY

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**ABSTRACT.**—Winter territory size in the Sanderling (*Calidris alba*) on marine beaches varies inversely with prey density. Multivariate analyses suggest that the inverse correlation results indirectly because more intruders are attracted to areas of higher prey density, and increased intruder frequency makes territorial defense more costly. Once the interaction between prey density and intruder density is controlled statistically, prey density has no effect on territory size. *Received 8 January 1979, accepted 29 March 1979.*

THE sizes of territories defended by many animals show large intraspecific variation. Where measurements have been obtained, territory size often relates inversely to food abundance: smaller territories occur in areas of higher prey density (Pitelka et al. 1955, Stenger 1958, Moss 1969, Clarke 1970, Holmes 1970, Maher 1970, Watson and Moss 1970, Stimson 1973, Slaney and Northcote 1974, Gill and Wolf 1975, Simon 1975, Gass et al. 1976, Salomonson and Balda 1977). These results, suggesting that food resources exercise proximate control over the expression of territorial behavior, have played a central part in the historical and often tempestuous arguments over the ultimate adaptive benefits of territoriality (Hinde 1956, Pitelka 1959, Brown 1964, McLaren 1972, Wilson 1975, Verner 1977, MacLean and Seastedt 1979, Rothstein 1979).

Although the relationship of territory size to its food value is commonly cited as a general pattern, there have been few attempts to identify the proximate mechanisms by which this pattern is brought about. Two hypotheses have been proposed: under hypothesis 1, an animal assesses prey density and directly adjusts territory size to include resources sufficient for its energetic needs plus, possibly, some unspecified increment for a long-term insurance of a reliable food supply (Armstrong 1965, Stimson 1973, Brown 1975, Simon 1975, Gass et al. 1976, Salomonson and Balda 1977). This hypothesis is the most widely accepted. Under hypothesis 2, an animal defends an area as large as it can, but its territory size is constrained by competition (Hinde 1956, Lack 1966, Krebs 1971, Schoener 1971, Dunford 1977). Areas of higher prey density attract more competitors and are more costly to defend; thus residents defend smaller territories. By this hypothesis the inverse relationship between territory size and prey abundance results indirectly through an intervening variable.

Historically these two hypotheses have been viewed as mutually exclusive alternatives, but this need not be the case. Work by Gill and Wolf (1975) and Kodric-Brown and Brown (1978), among others, suggests that territory size determination may actually involve a balance between the benefits (hypothesis 1) and the costs (hypothesis 2) of defense.

In this paper, we test these hypotheses through a multivariate analysis of winter territorial behavior in nonbreeding Sanderlings (*Calidris alba*) on ocean sand beaches at Bodega Bay, California. Specifically, we consider the relationships between prey

density and intruder density and then examine their effects on territory length. Our results strongly support the second hypothesis.

Since 1974 we have studied Sanderling winter spacing behavior on outer coast beaches in central coastal California (Myers et al. 1979a, b; Pitelka et al. 1979; Connors et al. MS). Sanderlings at Bodega Bay use local beaches largely during tide heights greater than 90 cm, moving to sandflats in a nearby lagoon at lower tide levels. While on the beach, they frequently defend linearly arranged territories from 10 to 120 m long within the wave-washed zone. Observations of color-banded individuals indicate that a Sanderling may defend the same site during each tidal cycle for several months, but often it does so for briefer periods of 1–20 days. Some birds return to the same territory during successive winters after migrating to and from their arctic breeding grounds. Yet many birds (30–90% of the same local population) forage in roving flocks near the territorially defended sites. These nonterritorial birds often enter the territories and evoke aggressive supplantations by the territorial occupants.

Individual Sanderlings switch repeatedly between territorial and nonterritorial behavior. Thus usually within the flocks of nonterritorial birds are individuals that defended in the past or will defend in the future. For the birds occupying territories at the moment, these potentially territorial birds may represent an acute source of competition for the defended sites.

Both territorial and nonterritorial Sanderlings are site-faithful during winter. Returns from color leg-banding indicate that almost all individuals remain in the Bodega Bay region throughout the winter and that a high proportion (approximately 70% of all adults) return the subsequent year.

#### METHODS

Our previous years' experience with Sanderlings in the study area indicated that beach conditions and Sanderling behavior can change quickly with the onset of a storm. This fact dictated that the sampling be compressed into as short a time period as possible. Fortunately, no such changes interrupted the sampling.

From 2 to 4 February 1977, we measured prey densities, mapped territories, and censused territorial and nonterritorial birds along 1,300 m of Salmon Creek Beach, an outer coast beach at Bodega Bay (Fig. 1). The beach had been divided into 50-m units marked by permanent stakes. We made density measurements for each variable serially within each unit using a methodology developed during trials in the previous year.

The only Sanderling prey species encountered regularly during the sampling on Salmon Creek Beach within areas where Sanderlings foraged was the isopod *Excirologana linguifrons* (Richardson). Our previous sampling of *Excirologana* revealed pronounced intertidal zonation, with peak densities in the upper intertidal zone (Connors et al. MS, see also Dahl 1952, Klapow 1971). To compare densities in different beach units, we sampled 27 cross-tidal transects during low tide extending from the previous high tide line to low water, one at each 50-m stake. Along the cross-tidal transects we located the center of the *Excirologana* zone by taking single samples every 5 m beginning at the high tide line. Each sample consisted of three pooled cores with core size being 101 mm diameter by 78 mm deep. Samples were sieved through a 1-mm screen, and animals were counted in the field. At the center of the *Excirologana* zone thus identified, we collected four additional replicate samples, each separated along the beach by 2 m. The average of the five replicates taken at the zone center was used as an estimate of peak density for that location along the beach. This sampling procedure was repeated on Doran Beach (Fig. 1) in late winter 1978 (see below).

Intensive mapping of *Excirologana* densities on finer scale grids (basic units of 1 × 1-m, 2.5 × 2.5-m, and 2.5 × 10-m sizes) over 25- and 50-m lengths of beach indicated that although our peak density estimates may have obscured some fine-scale variation in prey density, they adequately reflected the major variations in density along the beach. Measurements were made at low tide even though Sanderlings used the beach during high and intermediate tides (Connors et al. MS), because (1) sampling when

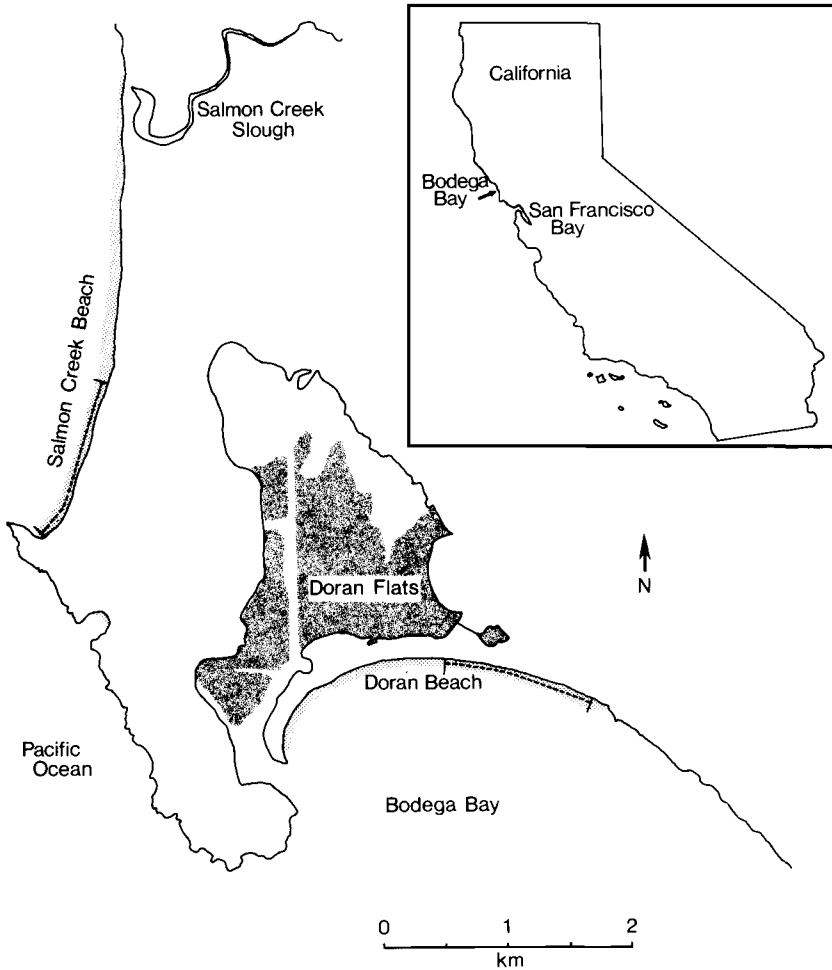


Fig. 1. Map of the study area near Bodega Bay, California. Even stippling shows the distribution of sandy beaches in the area. Darker, uneven stippling identifies harbor sandflats exposed as tide recedes. Dashed lines indicate positions of study plots. Inset shows the position of Bodega Bay within California.

the birds were present could potentially interfere with their behavior, and (2) sampling was safer and more efficient once the *Excirolana* zone was out of the surf. We had previously tested our sampling technique for changes in *Excirolana* density between high and low tides at sampling locations along cross-tidal transects and found no significant differences between the means of replicates taken at the same positions.

We chose the 78-mm core depth, which exceeds the probing depth of Sanderlings, because the isopods move down vertically in the substrate as the tide recedes (Jones 1970, Klapow 1971, Myers et al. unpubl. data). Thus prey available at high tide move below Sanderling probing depths at low tide. The 78-mm core takes samples to the penetration depth of most if not all *Excirolana* at low tide.

Twice each morning during high tide, prior to prey sampling, we censused Sanderlings foraging within the study area, recording the numbers of birds in each 50-m section of beach and classifying birds as territorial or nonterritorial based on their responses to other birds and their uses of territorial displays (Myers et al. 1979a, Connors et al. MS). During the high tides we also mapped territorial boundaries by observing fights between neighbors and by recording the positions at which intruders entering a territory elicited responses from the resident. We used this same procedure on Doran Beach (Fig. 1) in late winter 1978 in conjunction with our repetition of the prey sampling (above).

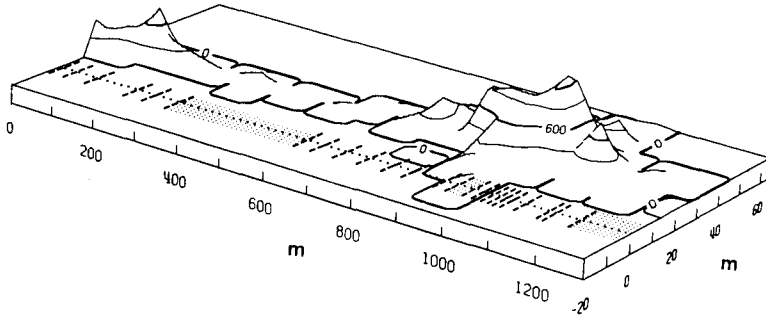


Fig. 2. Spatial distribution of *Exciorolana linguifrons* and Sanderling territories along 1,300 m of outer coast beach near Bodega Bay, California, 2–4 February 1977. The viewer sees the surface from land looking out to sea. The long axis runs along the beach, while the short axis is cross-tidal. The high tide line (artificially straightened for display purposes) is marked by the dotted line in the foreground at 0. Surface height indicates density (*Exciorolana*/m<sup>2</sup>) with contour lines every 300 *Exciorolana*/m<sup>2</sup>. Territory boundaries are shown with dashed lines at the high tide line. Territories were defended over the *Exciorolana* zone, but boundaries are cut short above the zone here so as not to confuse the figure. Stippling identifies undefended areas.

From these data we determined territory length (TL), intruder density (ID), and prey density (PD). ID for each territory was calculated as the average number of nonterritorial Sanderlings recorded within the 50-m unit in which the territory was located. When a territory extended over more than one unit, we assigned it the average of ID for the units involved, weighted by the relative proportion of the territory in adjacent units. PD for each 50-m unit was determined as the average of *Exciorolana* densities from cross-tidal transects at each end of the unit. We then assigned to the territory an estimate of PD based on the average value for the 50-m units contained within the territory.

Analyses were run at the U.C. Berkeley Computing Center. Statistical tests were performed using programs from SPSS (Nie et al. 1975).

## RESULTS

*Sanderling and Exciorolana densities.*—Along Salmon Creek Beach during the high tide censuses we mapped 21 territories ranging in length from 10 to 90 m and averaging 41 m (Fig. 2, Table 1). Eight of the 21 territorial birds had been captured previously and marked with unique combinations of colored leg-bands. These individuals defended their territories throughout the high tides sampled over the 3-day period. Their persistence was consistent with our previous observations on territorial Sanderlings in the winter at Bodega Bay (Myers et al. 1979a).

Nonterritorial bird density (ID) averaged 11.5 intruders/50-m unit (Table 1). The maximum number of nonterritorial birds recorded during a given census was 164 birds. Twenty-six of these had been color-banded previously. Most of the nonter-

TABLE 1. TL, ID, and PD on study plots during February 1977 and March 1978; means with 95% confidence limits.

	Salmon Creek Beach, February 1977	Doran Beach, March 1978
TL (m)	41 ± 10	82 ± 14
ID (intruders/50 m)	11.5 ± 7.4	0.5 ± .4
PD ( <i>Exciorolana</i> /m <sup>2</sup> )	580 ± 160	671 ± 130
Number of territories	21	15

TABLE 2. Simple correlation coefficients and probability levels for measured variables.

Variable	PD	ln(ID + 1)
1/TL	.43 (0.003)	.72 (0.001)
PD	—	.62 (0.001)

ritorial birds congregated over a 400-m stretch of beach, located in Fig. 2 between 800 and 1,200 m. Average ID within this region reached 45 birds/50-m unit. Elsewhere along the transect, nonterritorial birds occurred only in low density, and individuals usually did not remain long in an area.

*Excirolana* density (PD) averaged 371 animals/m<sup>2</sup> over the entire transect; within areas defended by Sanderlings it averaged 580 animals/m<sup>2</sup> (Table 1). PD varied greatly along the beach (Fig. 2): while densities over much of the beach remained below 300 animals/m<sup>2</sup>, in some areas they exceeded 1,000 animals/m<sup>2</sup>. Variation among cross-tidal transects was highly significant (ANOVA,  $F_{26, 81} = 19.9$ ,  $P < 0.001$ ).

*Relationships among PD, ID, and TL.*—To examine relationships among the variables, we first calculated simple correlation coefficients between PD, ln(ID + 1), and 1/TL (Table 2). We chose these transformations for the following reasons: ln(ID + 1) was used because we expected the *per capita* effects of intruders to decrease at larger flock sizes. For example, the effect of adding one bird to an intruding flock of 20 Sanderlings will have less effect on the territorial resident than would adding one bird to a territory that had lacked intruders altogether. We used 1/TL because we expected a hyperbolic relationship between prey density and territory size (Gass et al. 1976). While these transformations reduced the sum of squared residuals compared to analyses performed on untransformed data, they did not alter the qualitative results.

The results indicate that territories are shorter in areas of higher food density ( $P < 0.01$ ). In this regard, they parallel results from previous studies (e.g. Stenger 1958, Simon 1975, Gass et al. 1976, Salomonson and Balda 1977). We also find, however, that nonterritorial bird density (ID) is greater in areas of higher food density ( $P < 0.001$ ), and further, that territories are smaller where there are more nonterritorial birds ( $P < 0.001$ ).

To unravel the interactions among the three variables, we performed partial correlation and multiple regression analyses. Our results are summarized in Table 3 and Fig. 3. They show that once the interaction between PD and ID is controlled statistically, the effect suggested by the simple correlation between PD and 1/TL disappears: controlling for ID, the partial correlation of 1/TL with PD is not significant ( $P > 0.4$ ). In contrast, the partial correlation of ln(ID + 1) with 1/TL while controlling for PD is highly significant ( $P < 0.001$ ).

TABLE 3. Partial correlation coefficients for 1/TL with PD and with ln(ID + 1).

Variable	Controlling for	Partial correlation coefficient	Significance
PD	ln(ID + 1)	-0.03	$P > 0.4$
ln(ID + 1)	PD	0.64	$P < 0.001$

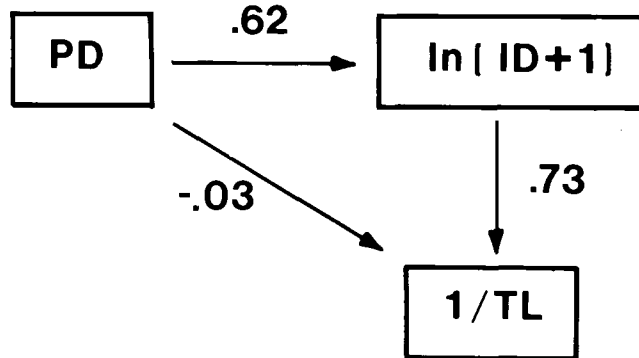


Fig. 3. Path diagram showing the relationship between prey density (PD), intruder density (ID), and territory length (TL). Path coefficients are standardized partial regression coefficients predicting  $1/TL$  from PD and  $\ln(ID + 1)$ .

Figure 3 displays the results of the multiple regression analysis as a path diagram (Wright 1921, Nie et al. 1975). We use this technique to construct a plausible, causal model of the interactions among the three variables based on their observed statistical relationships. The model must be viewed cautiously because of the difficulties of inferring causality from statistical correlations (Nie et al. 1975). The path diagram shows results consistent with the outcome of the partial correlation analysis. Standardized partial regression coefficients of  $1/TL$  with  $\ln(ID + 1)$  and PD, respectively, are 0.73 ( $P < 0.001$ ) and  $-0.03$  ( $P > 0.9$ ). The multiple correlation coefficient of  $1/TL$  with  $\ln(ID + 1)$  and PD is 0.72 ( $P < 0.002$ ). The path diagram thus suggests that variation in intruder density has a strong direct effect on territory size. Variation in prey density, on the other hand, has no effect, except for that occurring through the effect that prey density has on intruder density: where there are more prey, there are more intruders.

*Corroborative evidence.*—A special feature of the Sanderling's environment at Bodega Bay provided additional support for the importance of intruder density in determining territory size. In February 1978 an alternative feeding site became available at high tides. Salmon Creek Slough (Fig. 1), a small estuary seasonally separated from the ocean by a sandbar, was opened by winter storm waves and increased rainfall, exposing mudflats harboring high densities of amphipods. We repeated our sampling protocol (see Methods) along a 1,200-m transect on Doran Beach (Fig. 1) on 28 February and 1 March 1978 in order to exploit the circumstance of a high food density on a beach in conjunction with recent exposure of another food-rich site (Salmon Creek Slough). Except for some territorial birds that remained on Doran Beach, most of the Bodega Bay Sanderlings foraged at high and mid-level tides in Salmon Creek Slough. Thus nonterritorial Sanderling densities on the beach were markedly reduced. This change occurred despite the fact that *Excirolana* density was indistinguishable from the level measured on Salmon Creek Beach in February 1977 (Table 1;  $t = 0.83$ ,  $df = 34$ ,  $P > 0.4$ ). Additionally, there was a second prey species on this beach, megalops of the sand crab *Emerita analoga* (Stimpson), with an average peak density of  $38/m^2$ .

Under these conditions—low intruder density and similar if not greater prey density (including *Emerita*)—territory size doubled (Table 1;  $t = 5.08$ ,  $df = 34$ ,  $P <$

0.001). We interpret the increase in territory size as a response to decreased intruder pressure: the average intruder density in March 1978 was lower by a factor of 10 (Table 1;  $t = 3.07$ , assuming unequal variances,  $df = 20$ ,  $P < 0.01$ ).

We did not include these data in the first multivariate analysis because of the complications introduced by the additional prey species and by changing seasons and study plots. We can do so, however, by including *Emerita* density directly as another predictor variable. If we do combine both data sets into a single multiple regression, the results strengthen our conclusions: the multiple correlation coefficient rises to 0.77 ( $n = 36$ ,  $P < 0.001$ ), with the standardized partial regression coefficients for  $\ln(\text{ID} + 1)$ , PD (*Excirolana*), and PD (*Emerita*) being 0.71 ( $P < 0.001$ ),  $-0.02$  ( $P > 0.95$ ), and  $-0.09$  ( $P > 0.60$ ), respectively. Within the Doran Beach data set itself, there are no significant correlations, probably because of the low variation in both dependent (TL) and independent (ID, PD) variables compared to the Salmon Creek Beach data.

#### DISCUSSION

*Territory size.*—Our results are consistent with hypothesis 2: territory size in wintering Sanderlings is set proximally by the costs of defense. Because the results are correlational, they must be interpreted cautiously, but they clearly are inconsistent with hypothesis 1. Thus the simple inverse correlation between territory size and food density in this species results indirectly because areas of higher prey density attract more competitors and are therefore more costly to defend. The results suggest that a territorial Sanderling defends as large an area as possible, but the size it defends is constrained by increased competition in areas of higher food density. Thus while resource density remains a driving variable in this system, variation in territory size results from the proximate influence of intruder pressure.

The role of intruder density in the proximate control of Sanderling winter territory size was not, in itself, surprising. From the beginning, our observations suggested that the persistent incursions into defended areas by nonterritorial birds affected the time-activity budgets of resident territory holders. When one or a few birds entered the territory, the resident quickly dispatched the intruders, supplanting them with calls and aggressive chases. When flocks numbering more than a few birds (from 5 to 80+) entered, however, the resident often ceased chasing after a few minutes of frantic aggression. It then foraged within the flock, only intermittently showing aggressive displays or brief flurries of chasing. The potential effect of intruding flocks on the territorial birds was particularly high in those areas where the flocks tended to return day after day—the areas with highest prey density. In these areas, attempts at territorial defense were eventually abandoned. In contrast, territories on the beach away from the foci of flock activity—areas with lower prey density—suffered little intrusion.

Increasingly, theoretical treatments of territory size variation stress balances between costs and benefits of defense (Kodric-Brown and Brown 1978, MacLean and Seastedt 1979). Thus the lack of direct influence by prey density in our results is unexpected. Might Sanderlings be unique in this respect? We think not, but do acknowledge that three features of their winter system may make them an extreme case. One striking characteristic of Sanderling winter spacing patterns is the constant presence of nonterritorial birds. This may strengthen the relationship between intruder density and prey density and thereby exacerbate competition for preferred

sites. Yet even in species lacking a conspicuous, nonterritorial component in their local populations, residents must compete to establish their territories and then maintain defense throughout residency. A potentially important role for competition in setting territory size remains, but the flexibility in spacing behavior apparent in Sanderlings during the winter can, of course, operate more freely in a territorial system uncomplicated by breeding commitment to a site.

A second feature of the Sanderlings' system is that they obtain part of their daily energy from sources away from the territory (Myers et al. 1979a, Connors et al. MS). This characteristic is shared with other shorebirds defending nonbreeding territories in tidal environments. Its effect may be to reduce their dependence on resources contained within the territory and perhaps, thereby, to decrease their need to adjust directly beach territory size to prey density.

A third point concerns the high degree of environmental variability faced by Sanderlings on coastal beaches. The lack of sensitivity of Sanderling territory size to prey density may be a result of behavioral tactics used by territorial Sanderlings to insure themselves against varying costs and benefits for defense. We examine this hypothesis at length elsewhere (Myers et al. 1979b). Briefly, prey and intruder densities can fluctuate greatly over short time spans. In fact, because of winter storms' effects on prey distributions, current prey densities are poor predictors of what prey density will be in the future. This temporal variation requires a territorial bird either to track the changes in prey and intruder densities through time by adjusting its territory size frequently, or to defend a size large enough so that it will encompass sufficient food to warrant and permit continued defense, even though the territory may often contain far more food than is required. The comparison of Salmon Creek Beach and Doran Beach prey densities indicates that this may occur frequently. We suggest that Sanderlings choose the second tactic because of the rate of change in prey density and the difficulty of expanding territory size in response to decreased prey density, especially when neighboring territorial birds must expand also.

The significance of these results rests in our ability to measure TL, ID, and PD simultaneously. No previous studies of territorial behavior have achieved this multivariate perspective. We must ask, however, to what extent our interpretation depends on the relative ease of measuring ID versus the difficulty of measuring PD, a variable that has proven problematical in many ecological studies. Although we acknowledge that our results must be interpreted cautiously, the strong positive correlation between  $\ln(\text{ID} + 1)$  and PD (Table 2, Fig. 3) suggests that our measurements of PD reflect variation in PD to which foraging Sanderlings respond. We also point to the corroborative evidence from Doran Beach (Table 1) as strong support for our results and interpretation.

*Territory placement.*—Sanderlings defended territories in two areas along the Salmon Creek Beach plot, between 0 and 300 m and between 600 and 1,200 m (Fig. 2). Gaps in the territorial array occurred where *Excirolana* density was low (under 200 animals/m<sup>2</sup>), but a gap was also located in the area of high *Excirolana* density (exceeding 1,200 animals/m<sup>2</sup>). Clearly, the probability of territorial behavior was not a simple increasing function of food density.

This pattern of defense at intermediate food densities resembles the observations by Carpenter and MacMillen (1976) and by Gill and Wolf (1975) for two different species of nectarivorous birds. The first authors modeled their observations on an Hawaiian honeycreeper (the Iiwi, *Vestiaria coccinea*) in terms of lower and upper



thresholds on territoriality. According to their interpretation, birds did not defend below a lower limit of food abundance because energetically they could not support their basic maintenance costs. Above the upper threshold they stopped defending because food became superabundant, and defense was no longer required in order for a bird to obtain the energy it required. Gill and Wolf's analysis of Golden-winged Sunbird (*Nectarinia reichenowi*) behavior rested upon a hyperbolic relationship between food density and foraging rate, and the effect of defense on nectar availability: at increasing nectar levels, birds received smaller returns from their defense efforts, until finally the costs of defense exceeded the energetic benefits.

Our observations do not allow us to choose between these models. The data are few, and further, we know too little about the foraging or energetic relationships of a Sanderling to calculate at what point a resource becomes superabundant. Nor can we specify the relationship between food density and foraging rate with sufficient precision to determine whether the Gill and Wolf model is applicable. Our observations do suggest that the costs of defense contribute significantly to the observed pattern. Even though no individuals consistently defended sites within the region of high *Excivolana* density, aggression did occur repeatedly. Different individuals, some color-banded, were involved at different times, and there did not appear to be any consistent spatial pattern in the aggression. We suspect that any resident attempting persistent defense would have been swamped by nonterritorial intruders, becoming either unable to derive benefits in excess of the costs of defense or simply physically unable to defend because of the large numbers of intruders. In the Sanderling system, then, territories may become indefensible at higher prey densities because of the strong, positive relationship between PD and ID.

Gill and Wolf (1975) recognize this possibility, as do Kodric-Brown and Brown (1978). Robertson et al. (1976) report similar patterns in fish, as does Bailey (1978) for frugivorous birds. Carpenter and MacMillen (1976) disavow the importance of defense costs in setting the upper threshold for their honeycreepers. We suggest that their system requires further study, especially in regard to the relationships between resource density and intruder pressure.

*Implications for the adaptive significance of territoriality.*—In prior studies, inverse relationships between food density and territory size have been interpreted as evidence for the food-based nature of vertebrate territories (e.g. Stenger 1958, Smith 1968, Holmes 1970, Simon 1975, Salomonson and Balda 1977, MacLean and Seastedt 1979; but see Verner 1977). Definitive tests of this hypothesis, however, cannot rest on simple correlations between territory size and food abundance, because these relationships derive from proximate constraints on territorial behavior as well as from its ultimate selective benefits. First, as our results caution, the simple correlations may arise indirectly through intervening variables. And second, the fact that a territorial animal must gain sufficient energy to support its activities places proximate limits on its activities independent of the ultimate benefits for defense. Thus, if an animal obtains all of its energy from sources on the territory, then minimum territory size must be larger in areas of lower food density, even though food *per se* may not provide the selective impetus for territoriality.

The interactions of prey density, intruder density, and territory size that we report here demonstrate the need to separate factors exercising proximate control over territory size from those contributing to the selective basis for the behavior itself. We do not imply that food is not of fundamental importance to a territorial bird.

In fact, we argue elsewhere (Myers et al. 1979a, b) that shorebird winter territories are food-based. Rather, we pinpoint a fallacy in the logic often applied in studying the evolution of territoriality.

### CONCLUSIONS

Our results show that Sanderling winter territory size relates inversely to resource density, but only indirectly through the attraction of intruders to areas with more prey. These sites are therefore more costly to defend. Further, the results indicate that both prey and intruder densities influence the distribution of territories along a beach, with defense occurring at sites of intermediate prey abundance. Clearly, we need comparative studies of the potency of intruder pressure in the regulation of territorial behavior in other species, especially those with social systems less fluid than that of wintering Sanderlings.

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