

TERRITORIALITY IN NON-BREEDING SHOREBIRDS

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ABSTRACT.—During the non-breeding season, many shorebirds defend feeding territories. Our studies in coastal California and eastern Argentina examine the extent of shorebird 'winter' territoriality, and describe its ecological context. Eleven species in California and 13 in Argentina defend territories for varying periods of up to several months' duration. The expression of territoriality differs in extent between species, individuals, and habitats, being most strongly developed in local populations foraging on the short-grass pampas and seasonal wetlands of coastal Argentina. Explanation of this variation may best be sought in terms of individual responses to local habitat conditions affecting the energetic costs and benefits of defending foraging sites. One such habitat parameter appears to be the length of time that local areas are available for foraging. Other hypotheses, such as preparing individuals for breeding behavior or decreasing predation risk, are considered and tentatively rejected.

Many shorebirds defend territories in the winter. Yet their activities frequently pass unnoticed, overshadowed by the spectacular size and unison of nearby winter shorebird flocks. The striking contrast between these two spacing strategies, often juxtaposed across a defended boundary, poses a fundamental ecological and evolutionary question: Why should a bird indulge in territorial defense while others survive nonaggressively? In this paper we establish a framework for considering this question by examining the characteristics and extent of shorebird non-breeding territoriality.

Our data stem from several seasons' work in two localities, including 18 months observing North and South American species overwintering in coastal Buenos Aires Province, Argentina, and three winters at Bodega Bay in central coastal California. During these studies we have concentrated on the White-rumped (*Calidris fuscicollis*) and Buff-breasted (*Tryngites subruficollis*) sandpipers in Argentina, and the Sanderling (*Calidris alba*) in California, switching opportunistically to other species as circumstances permitted. In addition we draw upon many field seasons with breeding and migrating shorebirds along the arctic coast of Alaska.

Territorial non-breeding shorebirds obtain control of resources within a defended area through aggressive spatial defense. In many cases an individual gains exclusive use of the area; in others, however, it does not exclude all intruders successfully. The defended site is usually fixed, with persistent boundaries that are defined by referents external to the aggressing bird. In both these respects territorial wintering shorebirds meet the most stringent criteria for territorial behavior (Noble 1939, Pitelka 1959, Wilson 1975). But they also deviate from its classic form. In fact, individual variability is so common in such central characteristics of winter shorebird territoriality as size of territory, duration and consistency of defense, dependence on territorial resources, etc., that the variation itself must be acknowledged as an essential feature of the spacing pattern. As will become evident below, the variation also serves as a useful tool for dissecting the possible benefits or costs of territorial behavior. Through this review, therefore, we will emphasize not only the characteristics of winter territoriality but also its patterns of variation.

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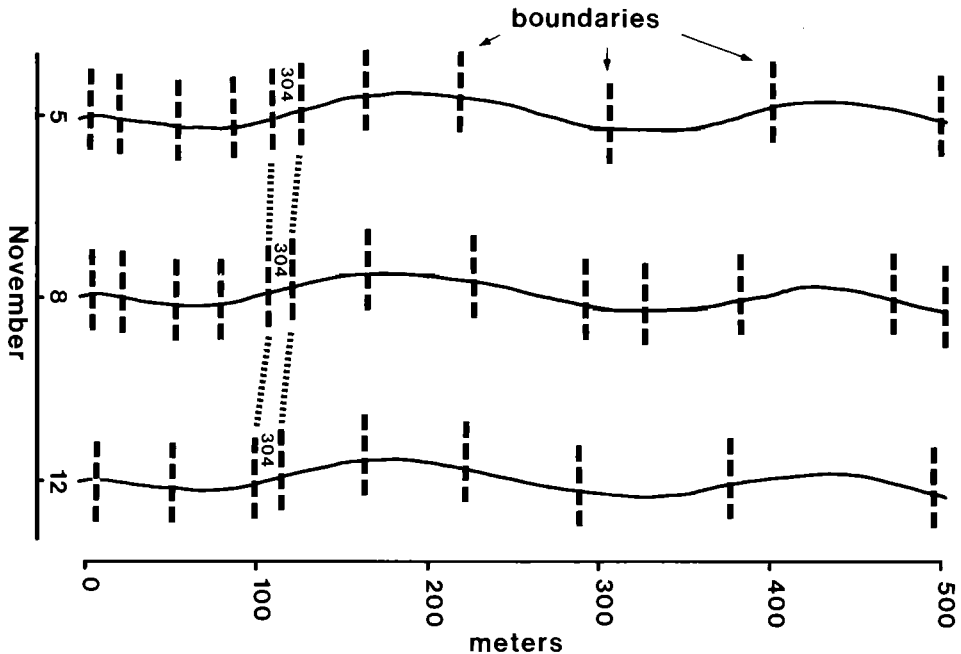


FIGURE 1. Positions of territorial boundaries defended by *Calidris alba* over 500 m of outer beach transect near Bodega Bay, California, on three days during early November 1976. Number 304 is a color-banded bird territorial on the transect during November.

FEATURES OF SHOREBIRD NON-BREEDING TERRITORIALITY

TERRITORY STABILITY

Most shorebird territories have well-defined boundaries about which border fights occur regularly. After watching a series of interactions between neighbors at a border, an observer can often predict with considerable accuracy when subsequent fights will occur, based on distance of the birds from the boundary. The site-specific nature of this behavior emphasizes an important distinction between territoriality and other forms of aggression: it is controlled by external referents, obviously in response to intruders violating an externally defined space rather than individual distance.

Boundaries are often so precisely and consistently defended for periods of several days or more that they take on an almost palpable quality. Hamilton (1959), for example, found boundary positions while working with migrant Pectoral Sandpipers (*Calidris melanotos*) in Manitoba that shifted less than 10 cm per day. We have similar observations for White-rumped and Buff-breasted sandpipers and Sanderlings. But territorial arrays can also be more fluid. Figure 1 illustrates the range in boundary stability of an array of Sanderling territories along a beach near Bodega Bay, California. One bird, No. 304, was banded; as the figure shows, its territory remained in the same location throughout the plotted interval, with only a few minor shifts in border position. The constancy shown

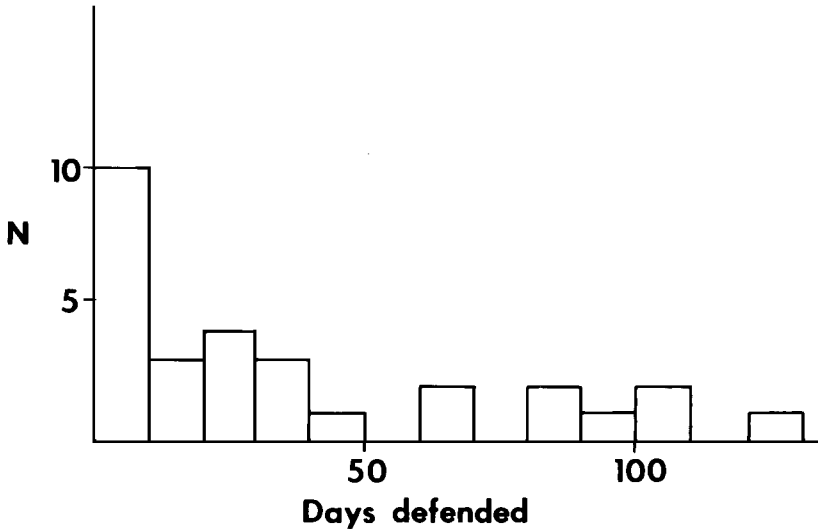


FIGURE 2. Minimum length of time in days that 31 territories were defended by color-banded *Calidris alba* on an outer beach near Bodega Bay, California, 1 October 1976 to 1 April 1977. Three individuals who switched territories at different times during the winter are treated as independent cases of defense for each site defended. All other individuals occupied only one territory per bird.

by many other boundaries on either side of No. 304 implies that other, unmarked birds remained consistent as well. Although this map suggests considerable stability in the array, some boundaries did change, shifting along the beach, disappearing entirely, or appearing de novo during the 8-day census period.

As an extreme example of shifting border position, Sanderlings also may defend an area around a foraging Black Turnstone, *Arenaria melanocephala* (Connors 1976). Occasionally a Sanderling will feed in close association with a Turnstone, working through substrate exposed by the Turnstone as it flips over beach litter. When the Turnstone moves, so does the territorial Sanderling, as does the focus of its supplantations. It is defending, in essence, a moving territory, with its aggression cued to the Turnstone's position.

Individuals vary with respect to the length of time that they defend a given territory. While some occupy sites for only a few hours, others will defend consistently for several months: individually color-marked White-rumped Sandpipers in Argentina defended territories up to two continuous months, with 14 holding territories for an average of 31 days (Myers 1976). Sanderlings can be even more persistent: during 1975, one remained territorial for seven months on an outer beach site near Bodega Bay (Connors 1976). In contrast, other Sanderlings at Bodega Bay switch locations, moving several hundred or more meters away and resuming defense in a new position. Still others, after maintaining territories for a period, may cease defense entirely. Figure 2 summarizes the length of time that 31 Sanderlings defended territories along the outer sandy beach at high tide. Many occupied sites for relatively short periods, with the mode lying under 10 days. A significant fraction, however, committed themselves for several weeks to the same location.

Consistent among-habitat differences suggest the importance of environmen-

TABLE 1
Calidris alba TERRITORY CHARACTERISTICS IN DIFFERENT HABITATS^a

| Habitat | N | Mean length | Range | Duration |
|------------------|----|-------------|---------|----------------|
| Beach | 31 | 41 m | 12–89 m | Up to 7 months |
| Sand flat | 5 | 27 m | 18–31 m | Up to 2 months |
| Beach flood pool | 25 | 5 m | 2–10 m | 1–2 hours |

^a Data from Bodega Bay and Santa Barbara, California.

tal factors in determining the length of territorial occupancy (Table 1). Birds clearly do not defend sites beyond a time when foraging is no longer possible. For example, Pectoral Sandpipers and other species using temporary vernal ponds in Argentina abandon their territories as the site dries (Myers and Myers 1979). But often the cause is less apparent: a territorial bird may stop defending a site yet continue foraging in the same location. Work in progress with Sanderlings at Bodega Bay suggests that cessation of defense relates to changing resource levels: territories may be defended over only a restricted portion of the range of resource densities encountered on a sandy beach, while nonterritorial foraging may take place under a broader set of conditions. As resource levels fluctuate, birds may respond by switching from one behavior to another. We suspect, however, that other factors such as predation and conspecific density also affect the likelihood of territorial defense (see below).

TERRITORY SIZE

Shorebird winter territories rarely approach a hectare in size (Table 2). As many shorebirds fly several kilometers between roosts and foraging sites, their defended areas are small compared with the scale of daily movements. They are also much smaller than breeding territories (Table 2). Despite their small size, individuals often confine most if not all foraging within territorial boundaries (see below).

Interspecific variation in territory size relates to body dimensions. In general, smaller species defend smaller territories. Table 3 presents ranges and means of

TABLE 2
 COMPARISONS OF BREEDING VS. NON-BREEDING TERRITORY SIZE (HECTARES)

| Species | Breeding | Non-breeding |
|--------------------------------|-----------------------|----------------------|
| <i>Pluvialis dominica</i> | 25 ^a | 0.1–0.3 ^b |
| <i>Charadrius semipalmatus</i> | 0.03 ^c | .01–.05 ^d |
| <i>Calidris fuscicollis</i> | 4 ^e | .01–.05 ^b |
| <i>Calidris melanotos</i> | 1.5–10 ^{a,f} | .01–.05 ^b |
| <i>Calidris alba</i> | 32 ^g | .01–.1 ^d |
| <i>Tryngites subruficollis</i> | 0.05–3 ^{h,i} | .01–.3 ^b |

^a Myers, Shuford, and Pitelka 1978.

^b Myers and Myers 1978.

^c Smith 1969 (estimated from Fig. 2, p. 185).

^d Myers, Connors and Pitelka, unpubl. data.

^e Parmalee et al. 1968.

^f Pitelka 1959.

^g Parmalee 1970 (actually a maximum breeding density; territories may not have been contiguous, in which case territory size would be smaller).

^h Pitelka, unpubl. data.

ⁱ Prevett and Barr 1976.

TABLE 3
LENGTHS OF WINTERING SHOREBIRD TERRITORIES ALONG LINEAR HABITATS (METERS)^a

| Species | N | Minimum | Maximum | Mean |
|------------------------------------|----|---------|---------|------|
| <i>Charadrius alexandrinus</i> | 2 | 70 | 145 | 108 |
| <i>Charadrius semipalmatus</i> | 5 | 16 | 30 | 20 |
| <i>Calidris alba</i> | 31 | 12 | 89 | 41 |
| <i>Charadrius vociferus</i> | 2 | 40 | 48 | 44 |
| <i>Pluvialis squatarola</i> | 4 | 80 | 155 | 125 |
| <i>Catoptrophorus semipalmatus</i> | 8 | 80 | 300 | 211 |

^a Data from Bodega Bay and Santa Barbara, California.

territory lengths along linear habitats for a number of species ranked in order of increasing body weight. The relationship holds except for the Snowy Plover (*Charadrius alexandrinus*). This general pattern is consistent with empirical and theoretical treatments of other taxa (Schoener 1968, Wilson 1975), suggesting that wintering shorebirds are not immune to the energetic constraints governing territory size in many animal groups.

The area-body size relationship overlays, nevertheless, considerable intraspecific variation in territory dimensions. Part of this variability can be partitioned to among-habitat differences: for example, along the beach swash zone Sanderlings consistently defend large territories compared to sites occupied either on beach flood pools or on protected sandflats (Table 1). But even within one habitat, individuals defend areas of considerably varying dimensions. Figure 1 illustrates the variation in this regard among Sanderlings on the outer sandy beach. In fact, during each day represented in Figure 1, Sanderlings occupied sites along this stretch of beach spanning much of the range in variation we have observed throughout 3 years of fieldwork with the species.

Fluctuating resource levels contribute to the variation in territory size both within and between habitats. Ongoing work with Sanderlings and their major sandy beach invertebrate prey reveals several significant interactions between territorial behavior and prey densities: territories are more likely to be established and are smaller where prey densities are higher (Myers, Connors, and Pitelka, in prog.). But other factors complicate this relationship, in particular the recruitment of nonterritorial birds to areas of exceptional prey density and the effect this has on costs of defense (see below).

AGGRESSIVE DISPLAYS

Among non-breeding shorebirds, territorial individuals persistently attack or display toward intruders with varying degrees of subtlety, from barely perceptible motions to prolonged physical contact. The intensity of territorial aggression can reach astonishing limits. In some species, particularly plovers, body blows with wings occasionally fell the attacked bird; for example, a border fight between two Rufous-chested Dotterels (*Zonibyx modestus*) in coastal Buenos Aires, Argentina, at first appeared to end when one bird landed a powerful blow to the other's head. The latter flew a few meters away only to collapse in water. Nevertheless, after remaining there motionless for several minutes, it staggered up to return to the fray. Such anecdotes only begin to convey the intensity and persistence of territorial interactions between wintering shorebirds.

Displays used in these aggressive interactions are often highly ritualized and vary little among related species. Scolopacids use slight changes in tail, wing, and back feather position in territorial display; Hamilton's (1959) description of tail-lowering in Pectoral Sandpipers resembles postures in the White-rumped Sandpiper, Sanderling, Buff-breasted Sandpiper, Willet (*Catoptrophorus semipalmatus*), Lesser Yellowlegs (*Tringa flavipes*), and Hudsonian Godwit (*Limosa haemastica*). Species differences often feature peculiar feather patterns of individual species: White-rumped Sandpipers will raise their tail while dropping their wings, exposing the white rump; Sanderlings uncover their black alular patch in aggressive situations.

Plovers rely more on direct physical interaction and parallel border marches than do sandpipers. Border displays used by *Charadrius* and *Pluvialis* plovers as well as the Rufous-chested Dotterel often entail a drooped wing preparatory to striking. The tail is fanned and tilted slightly so that its upper surface projects toward the opponent. Neighboring plovers march repeatedly back and forth in parallel along a border in this posture, wing toward opponent drooped, back feathers slightly raised, and tail fanned.

While different in specific attributes, shorebird territorial signals reflect basically similar display requirements of a territorial bird. Their displays thus fall into four functional categories: 1) displays used during chases and supplantations; 2) displays used in combat; 3) displays used to establish and negotiate boundary position; and 4) displays used to identify the individual as territorial and to specify the spatial contingencies of aggression. The most elaborate of these, and certainly those of longest duration, are signals exchanged between neighbors over boundaries, either in establishing, repositioning, or identifying boundary position.

The mere presence of a visible bird in open habitat is, in a sense, a form of announcement. But spontaneous advertisements comparable to those used by breeding males are markedly absent on winter territories: non-breeding territorial displays do not occur without provocation. This point bears upon functional and contextual differences between breeding and non-breeding territorial activities. First, breeding birds exclude competitors while simultaneously attracting a mate. Non-breeders, on the other hand, are unencumbered by any need to secure a nesting partner, and exclude all intruders. As a result, the breeding bird's displays possess a functional duality not shared by their winter counterparts. Second, the context of the displays differs between winter and summer insofar as it is set by the density of interacting individuals (Table 2). This affects the distances over which signals must be effective and the rates at which behavioral interactions occur. Thus, announcement displays on winter territories may be lacking because of the constant proximity and visual contact of neighbors and because of the already high rate at which intruders evoke other display types. If there are costs associated with spontaneous announcements, as can be expected given time-budget restraints and predator regimes, then it is really not surprising that winter repertoires lack this type of display.

These general differences in function extend to specific details of display form: winter displays appear to be specialized for the non-breeding context of high density, constant proximity, and good visibility. Despite extensive experience with several species both in the arctic and on wintering grounds, we observe few winter signals during nesting. The converse also holds; very few species employ

breeding displays in defense of non-breeding territories, even though breeding display activity does occur in winter flocks, particularly as spring migration approaches. Thus winter repertoires lack aerial displays (other than chases) or any complex vocalization. Those described above and drawn in Hamilton (1959) are among the most elaborate we have recorded.

The Buff-breasted Sandpiper deviates from this pattern by regularly employing some breeding displays on winter territories. This exception, however, may strengthen our argument because of the similarity in spatial scale between winter and breeding territory size for this species (Table 2). During the breeding season, males occupy sites in an exploded lek (Pitelka et al. 1974, Prevett and Barr 1976). They use several spontaneous displays to increase their conspicuousness to neighbors and potential mates, including a stylized flight pattern and ritualized jumping. Few of these spontaneous displays are used in the winter. Buff-breasted Sandpipers do, however, use a restricted set of wing postures in winter defense which are also employed in announcement on the breeding ground. The fact that winter encounters occur over similar distances and at comparable rates to breeding conditions may be important in allowing this shared repertoire.

For Semipalmated Plovers (*Charadrius semipalmatus*), the other species listed in Table 2 as having winter and summer territories of comparable size, the breeding data taken from Smith (1969) refer to areas used for nesting only. Most feeding occurred away from these sites. Information on the breeding display repertoire in Greenland where Smith obtained these data would be very interesting in this context. Near Barrow, Alaska, our primary arctic study area, individual Semipalmated Plovers usually occupy larger, noncontiguous territories defended with a wide-ranging display flight.

TERRITORIAL COMMITMENT

An individual bird invests time and energy into territorial defense, and in return obtains control over resources within its area. The magnitude of this territorial commitment differs among individuals, particularly with respect to the extent of dependence on territorial resources and the consistency of defense. By extent of dependence we mean the fraction of caloric intake necessary during a given time interval that is obtained on the territory. While this is difficult to assess directly, we estimate its magnitude by examining the proportion of foraging time that is spent on the territory, a quantity which shows great variation in territorial shorebirds.

In large part, cyclic environmental conditions set the daily patterns of territorial occupancy. Few if any birds spend continuous 24-hour periods on territories, as all are used within the context of a refuging system: territorial birds usually coalesce into communal roosts at night, or travel to other feeding areas when foraging on the territory is temporarily impractical. In nontidal areas, birds may defend throughout the daily foraging hours. For example, White-rumped Sandpipers fly up to several kilometers before dawn to territories in the inland wetlands of Argentina and remain until shortly after sunset (Myers 1976). Buff-breasted Sandpipers and Golden Plovers (*Pluvialis dominica*) defend territories in the Argentina Pampas grasslands throughout most of the day except for a period in mid-afternoon when they flock to local water holes (Myers and Myers, MS).

Complicated by tidal cycles, patterns of territorial occupancy in coastal areas

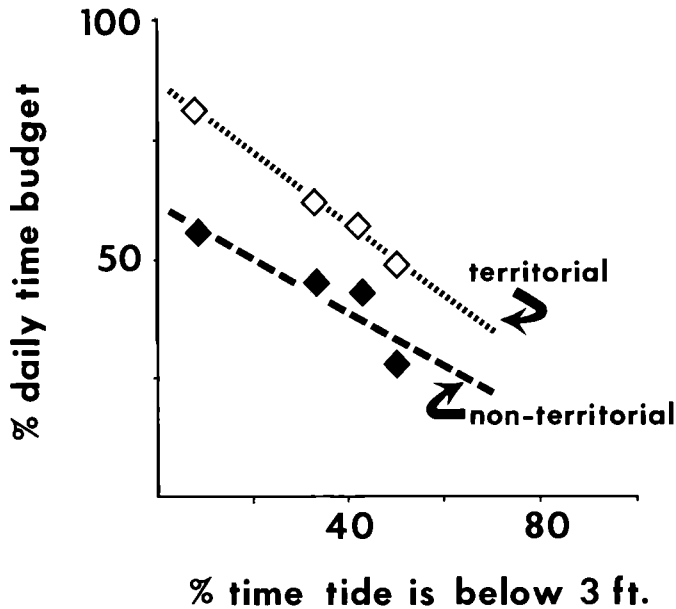


FIGURE 3. Percent daily time budget spent by *Calidris alba* on an outer beach near Bodega Bay, California, during different tidal regimes. Each point represents a separate day sampled dawn to dusk, November 1976. Percent daily time budget is a population estimate based on the maximum census obtained each sample day:

$$\% DTB = \frac{100}{nx_m} \sum_i^n x_i$$

where x_i = number of birds recorded during the i^{th} census; x_m = maximum census count for a given day; and n = number of censuses during a given day. Territorial and nonterritorial birds treated separately.

show far more variation. Individual birds of a few species remain on their territories during almost all tide heights. Some Willets, for example, adopt this schedule in salt marsh or along sloughs, rocky harbor shores, or on beaches. These sites share one important characteristic: they offer suitable foraging habitat over a wide range of tide heights, either because of complex ponding patterns or steep water edges with little horizontal displacement in water-line position as the tide moves out.

More commonly, a bird defends its territory during a limited period in the tidal cycle and then moves to other foraging areas as the water level changes. At similar tide heights during subsequent tidal cycles it returns to the territory. During the absence, few if any other conspecifics forage within its defended area because they too change feeding sites in response to tide levels. Sanderlings in the Bodega Bay region follow this general pattern throughout the winter. During high tides, they forage on sandy beaches, with many defending territories in fall and early winter (Fig. 1). As the tide drops, they fly to nearby harbor sandflats, moving individually or in small groups such that by low tide few remain along the beach (Connors 1976). Infrequently, individually marked birds may defend territories on the sandflats during low tides while also occupying beach territories during high tides.

Because of the relationship between foraging site and tide height, the proportion of the day spent on a territory depends upon tidal regime, i.e., the timing of tides in relation to daylight, and the relative amplitudes of high and low tide, variables which fluctuate over a lunar month. Data summarized in Figure 3 demonstrate this relationship: under all tidal conditions territorial Sanderlings devote a large proportion of their daily time budget to foraging on the territory, some individuals remaining for the entire day under appropriate tidal regimes much like the Willets mentioned above. But as the tidal regime changes and nearby sandflats lie exposed for longer periods, birds allocate less time to foraging on the beach territory (Connors, Myers, and Pitelka, in prep.). This changing pattern of use reflects but one time scale important in territorial dependence; another was examined earlier in discussing the length of time that birds remain territorial on a given site through the season.

Individuals differ both with respect to their dependence on territorial resources, as discussed above, and also in the consistency of defense. While many White-rumped Sandpipers in Argentina and Sanderlings around Bodega Bay normally respond without exception to intruders in their defended area, other individuals of these species, all color-banded, employ a behavior intermediate between classic territoriality and nonaggressive, site-specific foraging. These inconsistent birds fall into two general sets: some switch between episodes of strong defense and seemingly indifferent tolerance while others maintain a steady level of "half-hearted" supplantations, neither responding to all intruders nor cueing their behaviors as strongly to identifiable borders as do classically territorial birds. The likelihood of their aggression appears to be tied to a vaguely defined but fixed boundary zone and influenced by how close the intruder is to the resident. Their behavior thus falls between simple defense of individual distance and territoriality.

The source of this variation remains largely obscure. Individual differences based on sex or age class alone are insufficient predictors, as adult and juvenile or male and female birds all show the same range in behavior (Myers 1976, Myers, Connors, and Pitelka, in prog.). Variation in physical condition, including weight and hormonal levels, as well as past experience on the site in question may be involved. On the other hand, the consistent appearance of this ambivalent behavior in particular contexts suggests that it may be a response to environmental conditions: Sanderlings develop this pattern frequently in areas of high conspecific density while foraging on *Ulva* mats in protected sandflats or on thick mats of fresh, algal wrack along the upper beach.

Two special cases of switching between strong defense and nonaggressive tolerance can be linked directly to environmental factors: even the most consistent supplanter joins its neighbors in a compact flock when raptors fly over. Until the predator disappears, territorial aggression subsides and the flock remains together, although it may collect on an area normally defended territorially. Myers' (1976) data on dispersion in Buff-breasted Sandpipers document this clearly; territorial White-rumped Sandpipers, Sanderlings, and Golden Plovers behave similarly.

The second situation directly attributable to environmental control is seen in the response of territorial birds to invasion by a flock: while residents react at first with a burst of aggression, defense becomes sporadic and may stop if the

TABLE 4
GEOGRAPHIC RECORDS FOR TERRITORIALITY IN NON-BREEDING SHOREBIRDS

| Location | Species | Source |
|--------------------------------------|--|---------------------------|
| North Slope, Alaska | <i>Calidris pusilla</i> juveniles, <i>Calidris melanotos</i> | Myers and Connors, unpub. |
| Manitoba, Canada | <i>Calidris melanotos</i> , <i>Calidris pusilla</i> | Hamilton (1959) |
| San Francisco Bay region, California | <i>Calidris mauri</i> , <i>Calidris alba</i> , <i>Catoptrophorus semipalmatus</i> , <i>Charadrius semipalmatus</i> | Recher and Recher (1969) |
| La Jolla, California | <i>Pluvialis squatarola</i> | Michael (1935) |
| U.S. Atlantic coast | <i>Calidris pusilla</i> , <i>Calidris alba</i> | Recher and Recher (1969) |
| Scotland | <i>Tringa totanus</i> , <i>Numenius arquata</i> | Goss-Custard (1970) |
| Soviet Union | <i>Pluvialis squatarola</i> , <i>Charadrius mongolus</i> , <i>Tringa hypoleucos</i> , <i>Tringa cinereus</i> , <i>Tringa incana</i> , <i>Calidris ruficollis</i> | Panov (1963) |
| Denmark | <i>Vanellus vanellus</i> | Lind (1957) |

intruding group is sufficiently large (Myers, Connors, and Pitelka, in prog.). As long as the flock remains, the resident bird alternates between occasional chases and bouts of tolerant feeding. Color-marked territorial Sanderlings under these circumstances often maintain a low-intensity aggressive posture even while feeding in the flock, their tails slightly depressed and back feathers raised. We believe this pattern occurs because the flock effectively overwhelms the territory holder, increasing its defense costs beyond a supportable level. Our interpretation receives additional support from observations that if the flock disperses, spreading over several adjacent territories, the density of intruders on a given territory may fall low enough so that the resident again supplants all intruders. It will also renew consistent supplanting if the flock departs en masse. Robertson et al. (1976) interpret an interaction between schooling and territorial scarid fish similarly.

ALTERNATE STRATEGIES

The preceding discussion emphasizes a pervasive characteristic of winter shorebird spacing: a local population often contains a mixture of birds using space in different ways. Thus while up to 42% of marked local White-rumped Sandpipers foraging along a muddy stream in coastal Buenos Aires, Argentina, defended territories, the remainder of the same marked sample did not (Myers 1976). Similarly, 77 of 108 color-banded Sanderlings in Bodega Bay during the 1976-77 winter season never defended territories, while 31 did. Both Hamilton (1959) and Recher and Recher (1969) described similar patterns in other shorebirds, as did Davies (1976) for non-breeding pipits.

This heterogeneity in winter shorebird spacing must be explicitly incorporated into any analysis of their behaviors. For one, the varying extent of development of one strategy or another offers tantalizing clues as to their adaptive consequences (see below). But secondly, the very simultaneity of their expression opens an intriguing possibility: part of the payoff to birds of one behavior depends on the presence of the other and on the proportion of individuals in the

TABLE 5
 OCCURRENCE OF TERRITORIALITY AMONG WINTERING SHOREBIRDS IN CENTRAL COASTAL CALIFORNIA

| Species | Rocky intertidal | Sandy beach | Broad intertidal | Tidal slough, marsh | Inland wetland |
|------------------------------------|------------------|-------------|------------------|---------------------|----------------|
| <i>Pluvialis squatarola</i> | | t | t | t | |
| <i>Charadrius semipalmatus</i> | | nt | t | t | |
| <i>Charadrius alexandrinus</i> | | t | nt | | |
| <i>Charadrius vociferous</i> | | | ? | t | t |
| <i>Limosa fedoa</i> | | nt | nt | nt | |
| <i>Numenius phaeopus</i> | t | t | | | |
| <i>Actites macularia</i> | t | | | t | |
| <i>Heteroscelus incanum</i> | t | | | | |
| <i>Catoptrophorus semipalmatus</i> | t | t | t | t | |
| <i>Arenaria interpres</i> | | | nt | nt | |
| <i>Arenaria melanocephala</i> | nt | nt | nt | | |
| <i>Calidris mauri</i> | | | t | t | t |
| <i>Calidris minutilla</i> | | | nt | t | t |
| <i>Calidris alpina</i> | | | nt | nt | nt |
| <i>Calidris canutus</i> | | | nt | | |
| <i>Calidris alba</i> | nt | t | t | t | |
| <i>Aphriza virgata</i> | nt | | | | |
| <i>Limnodromus griseus</i> | | | nt | nt | |
| Percentage of species territorial | 57 | 62 | 38 | 67 | 60 |

* nt indicates no territorial birds of this species seen in this habitat; t indicates that a varying proportion of individuals defend territories.

population so behaving. A simple case entails the swamping phenomenon discussed above: given that territorial birds occupy the beach, others may gain access to otherwise unavailable foraging sites by joining in a flock and overwhelming the resident (Robertson et al. 1976). Formal applications of game theory considering territorial versus nonterritorial behaviors as possible evolutionarily stable strategies (Maynard Smith 1976) may be developed profitably.

EXTENT OF SHOREBIRD NON-BREEDING TERRITORIALITY

Even though little formal attention has been directed toward shorebird non-breeding territoriality, it has been reported from diverse geographic regions (Table 4). To these, we add records from coastal California (Table 5) and southern Argentina (Table 6). Taken together, these tables document its widespread occurrence across several continents and in many species. Among the territorial birds in both hemispheres figure representatives of many shorebird groups, including plovers, godwits, yellowlegs, and sandpipers. Of these, the charadriids and tringines are most frequently territorial: only one observed plover, the Tawny-throated Dotterel (*Oreopholus ruficollis*), never shows areal defense, while all five tringines (including *Catoptrophorus*, *Actitis*, and *Heteroscelus*) behave territorially.

Of 24 species commonly wintering along coastal California, we are sufficiently familiar with 18 to say that 11 of these 18 show a mixture of territorial and non-territorial behavior (Table 5). A similar pattern holds in the coastal zone of Buenos Aires Province, Argentina, where 13 of 19 well-observed species defend territories at least occasionally (Table 6). Territorial behavior occurs regularly in all

TABLE 6
 OCCURRENCE OF NON-BREEDING TERRITORIALITY IN COASTAL BUENOS AIRES PROVINCE, ARGENTINA

| Species | Sandy beach | Broad intertidal | Tidal slough | Inland wetland | Upland grassland |
|--|-------------|------------------|--------------|----------------|------------------|
| North American breeders | | | | | |
| <i>Pluvialis dominica</i> | | | | t | t |
| <i>Pluvialis squatarola</i> | t | t | t | | |
| <i>Limosa haemastica</i> | | nt | nt | t | t |
| <i>Tringa melanoleuca</i> | | | t | t | |
| <i>Tringa flavipes</i> | | | t | t | |
| <i>Calidris bairdii</i> | | | | t | nt |
| <i>Calidris fuscicollis</i> | | nt | t | t | |
| <i>Calidris melanotos</i> | | | | t | |
| <i>Calidris alba</i> | t | nt | | | |
| <i>Calidris canutus</i> | nt | nt | | | |
| <i>Calidris himantopus</i> | | | nt | nt | |
| <i>Tryngites subruficollis</i> | | | | | t |
| <i>Steganopus tricolor</i> | | | nt | nt | |
| <i>Arenaria interpres</i> | | nt | nt | | |
| South American breeders | | | | | |
| <i>Vanellus chilensis</i> | | nt | nt | t | ? |
| <i>Charadrius falklandicus</i> | nt | nt | t | t | |
| <i>Zonibyx modestus</i> | | nt | t | t | t |
| <i>Oreopholus ruficollis</i> | | | | | nt |
| <i>Thinocorus rumicivorus</i> | | | | | nt |
| Percentage of species territorial ^a | 50 | 11 | 55 | 83 | 57 |

^a *Vanellus chilensis* excluded from calculation for upland grassland.

habitats used by shorebirds in Buenos Aires Province except the broad intertidal (Table 6). This contrast emerges clearly in comparing the percentage of species territorial in each of the five habitat categories, with only 11% of species present in the broad intertidal establishing territories compared to an average of 61% in the other habitats. A χ^2 test based on the number of species territorial in each reveals significant among-habitat differences ($\chi^2 = 12.5$; $P < .03$). We have not made similar calculations for the coastal California area because our data for interior habitats are less complete.

The difference in Argentina is more striking still, because territoriality in the broad intertidal is unusual even for the one species defending mudflat sites, the Black-bellied Plover (*Pluvialis squatarola*). Elsewhere in coastal Buenos Aires, many species and many individuals defend territories; in several species the proportion of local populations behaving territorially is quite high. This is especially true with Golden Plovers and Buff-breasted Sandpipers in upland grasslands.

ADAPTIVE CONSEQUENCES

The ubiquity of non-breeding shorebird territoriality, as well as its striking features and their consistency among many species, poses a series of formidable problems: what factors influence a bird's decision to begin or cease defense? What generates the variability in individual behavior, or the population and species differences in degree of territoriality? What commitment does a bird de-

velop to its defended area, and how long does that last? Each of these involves fundamental questions about the behavior's adaptive significance.

An early analysis of shorebird winter territoriality argued for what essentially is the null hypothesis: Hamilton (1959) concluded that territorial behavior by migrant Pectoral Sandpipers was probably both residual from breeding behavior and nonadaptive in the winter context. We reject both of these arguments: first, non-breeding territoriality cannot be residual because birds which do not hold breeding territories will defend winter territories. For example, only adult male *Calidris melanotos* or *Calidris fuscicollis* hold breeding territories (Pitelka et al. 1974), yet juvenile *melanotos* as well as female and juvenile *fuscicollis* defend in the non-breeding season (Myers 1976). Female *melanotos* almost certainly do as well; one doing so simply has not yet been collected. Our observation of newly fledged Semipalmated Sandpipers (*Calidris pusilla*) fervently defending sites along the Alaskan arctic coast before their first migration further deflates the residuum hypothesis.

The second argument—that winter territoriality is nonadaptive—is more difficult to refute. If nothing else, the widespread and elaborate nature of winter territoriality stands against Hamilton's assertion. The energetic investment in establishing and maintaining territories must be considerable, as observations show that defense activities can occupy a significant portion of a territorial bird's time budget (Recher and Recher 1969, Connors 1976, Myers 1976). From what is known of the energy requirements of non-breeding shorebirds (Goss-Custard 1969) and suggested for the importance of the non-breeding period in the annual cycle of shorebird population regulation (Baker and Baker 1973), such an energy investment would be selected against were it merely nonadaptive.

Following considerations first posed by Brown (1964), we believe the key to understanding winter shorebird territoriality lies in the economics of defense. Benefits accruing to territorial behavior must be balanced with associated costs. In turn, the net profit or loss to territorial behavior has to be compared with results from a nonterritorial strategy. For the former to persist, not only must an individual be able to support its basic costs, but its behavior should also yield a more favorable balance than does nonterritoriality. Any mobile organism repeatedly faces this economic dilemma. And if the great variability in winter shorebird spacing behavior tells us anything, it is that the optimum solution changes rapidly over space and time. This general line of reasoning underlies more formal models developed by Gill and Wolf (1975) and Carpenter and MacMillen (1976) working with nectarivorous birds, although with the latter model there are also important differences.

Two sets of variables, energetic and risk, probably enter into a shorebird's benefit/cost "evaluation" of different spacing options. Their involvement is inescapable, both because of their conspicuous importance to shorebirds (Goss-Custard 1969, 1970, Page and Whitacre 1975), and because of their apparent importance in shaping spacing and social systems in general (Wilson 1975). But the relative importance of each, and the manner and direction in which they influence spacing behavior, promise to be central issues in the study of spacing patterns for some time.

Most shorebirds respond to predators by flocking, including those defending territories (Myers 1976). In light of Page and Whitacre's data on shorebird sus-

ceptibility to predators, this response appears to be highly adaptive. This suggests that the major influence of predation favors a flocking strategy: the individual should be less likely to defend a territory if by spacing out it increases its risk of predation. This increased cost of defense could, of course, be offset by increased energetic benefits accruing to the territorial bird.

Alternatively, predation might favor territoriality if shorebird antipredator strategies are hierarchically organized. In this view, the first line of defense might involve making the local area less attractive to a predator by keeping the density of conspecifics low, achieved via territoriality. This might reduce the amount of time a predator spends foraging locally. But once the predator is present, hunting in the area, the shorebird's behavior should change; the favored strategy for reducing predation risk might then be to flock together. In general, however, wintering shorebirds are not interspecifically territorial. If the principal benefit of territoriality derives from this lowered attraction of predators, advantages would accrue from eliminating other individuals of all species from the area. In fact, since winter territories are very small compared to the hunting range of avian predators, and conspecific flocks as well as other species are usually tolerated within the local area, overall shorebird densities are probably not sufficiently reduced to affect the likelihood of attracting the predator to the area. Thus from the available information we suggest that predation should be entered in the cost side of the territoriality equation.

The relevance of energetic considerations is also clear. Defense costs a bird directly because of caloric expenditures and indirectly by detracting from available foraging time. In turn, a bird presumably benefits by obtaining control over food resources within the territory, thereby reducing the rate at which competitors remove food. The ultimate payoff gained by this reduction in intruder cropping rate may derive either from short-term effects on availability of the food (e.g., Gill and Wolf 1975, Carpenter and MacMillen 1976) or long-term increases in food density or predictability (Goss-Custard, pers. comm.).

Many other variables may affect the energetic equations. In fact, the number conceivably involved is staggering, and certainly sufficiently large to produce the complex natural history we observe in shorebird winter territoriality. Several obvious candidates include food densities or dispersion (Gill and Wolf 1975, Carpenter and MacMillen 1976, Recher and Recher, 1969), resource renewal rates (Gill and Wolf 1975), intruder frequency (Schoener 1971), and the stability of local resourced through time (Horn 1968). Each may affect defensibility of a site by contributing to either costs or benefits. For example, we suspect that the last variable above figures heavily in setting the overall relationship between habitat type and dominant spacing behavior noted above. A simple case in point is the contrast between mudflats and upland grasslands: it simply does not pay to defend an area if the optimum foraging position will shift to a site 500 meters away within 30 minutes, before a bird can recoup the costs of establishing a territory. This relationship predicts that the percentage of birds territorial in tidal areas should vary with the rate of water line movement at particular sites. But it also assumes that the return on a territorial investment increases the longer that a bird can forage in the same place.

Most economic arguments, and certainly those centered around energetic considerations, assume that the payoff for non-breeding territoriality occurs within

the same season. Nevertheless it is possible that a bird gains from *winter* territorial behavior because of benefits accrued during the breeding *season*. While the behavior may not be adaptive within the winter season, a bird might defend a winter site because of some effect its winter behavior has on breeding performance, such as practice in defense, early pairing, etc. Although we cannot reject this hypothesis directly, it seems improbable because of the overall similarity of winter territorial strategies between species which differ remarkably in their breeding social systems (Pitelka et al. 1974). This indicates selection for winter territoriality independent of breeding events. The nonrandom distribution of territorial behavior over habitats argues likewise. If benefits do not depend on the winter situation, but rather develop only once the bird returns to breed, why should territoriality develop in some habitats and not in others? One possibility is that even though gross benefits may not depend upon the winter environment, costs may vary between habitats, such as those differing in predation regime. Changes in the net gain would then affect the probability of behaving territorially.

Finally, we turn to a theme developed by many papers in this symposium, that of shorebird dependence on coastal wetlands and the consequences of long-term decreases in type and extent of these habitats. In a local area, shorebirds move between a variety of habitats, often in cyclic daily routines such as done by the Sanderlings at Bodega Bay. Yet their movements shouldn't be viewed as evidence for an opportunistic way of life, nor should their apparent ability to exploit several habitat types be taken to suggest a lessened dependence on any given one: their welfare undoubtedly depends upon conditions across the whole mosaic. Removing part of that system will have effects beyond the local limits of disturbance because shorebirds depend upon it as an integrated whole. Shorebirds frequently develop long-term site faithfulness to winter regions, throughout a season and year after year (Connors 1976, Elliot et al. 1976, Kelly and Cogswell, this volume, Smith and Stiles, this volume). The widespread nature of winter territoriality indicates a dependence on local resources at an even finer scale. Thus a given sector of coast supports populations relatively attached to the area and utilizing it with a spectrum of behavioral strategies finely adjusted to local conditions. Taken together, these argue for a thoughtful reconsideration of the vagility normally associated with wintering shorebirds, and in turn on the birds' abilities to adapt to adverse environmental changes. We suggest that habitat disturbance will have impacts on shorebird welfare of greater magnitude and complexity than previously suggested.

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