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TERRITORIALITY AND FLOCKING BY BUFF-BREASTED SANDPIPERS: VARIATIONS IN NON-BREEDING DISPERSION

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ABSTRACT.—The spacing behavior of Buff-breasted Sandpipers was studied on their wintering grounds in coastal Buenos Aires Province, Argentina, from September 1973 to December 1974. Up to 2,000 Buff-breasted Sandpipers used the study area of 11,000 ha during austral spring of these years. Many defended non-breeding territories while feeding in the short-grass uplands even though they roosted communally in large monospecific flocks. Twenty-nine territories averaged 0.04 ha. The sandpipers moved between their feeding and roosting sites in flocks. They also flew daily during mid-afternoon to a nearby stream for water, often accompanying local flocks of American Golden Plovers. Defense of feeding sites continued throughout the day but it became less consistent during late afternoon. The appearance of a predator caused the sandpipers to flock, abandoning their territories. Shortly after the predator disappeared they returned to their feeding areas and resumed defense. Their responses to predators suggested that: (a) Buff-breasted Sandpipers benefitted from flocking because it decreased their predation risk; (b) the benefits for flocking related either to reducing the probability that they would be attacked or to reducing the attack success rate, not to increasing the likelihood of detecting a predator; (c) the benefits for territorial defense probably did not include reducing predation risk; and (d) sandpipers could simultaneously defend territories yet maintain the option of coalescing into a tight flock.

In general, wintering shorebirds feed in flocks. Lack (1968), Goss-Custard (1970a), and Stinson (1980) argued that this occurs because flock feeding reduces an individual's risk of being taken by a predator. Their interpretations are consonant with analyses of the advantages of group living in many mobile animals (Hamilton 1971, Vine 1971, 1973, Pulliam 1973, Alexander 1974, Powell 1974, Siegfried and Underhill 1975, Hoogland and Sherman 1976, Bertram 1978, Kenward 1978).

Direct observation indicates that an individual shorebird can lower its risk to predators by feeding within a flock (Page and Whitacre 1975). Individuals of many shorebird species, however, defend territories in their non-breeding seasons (Hamilton 1959, Recher and Recher 1969, Goss-Custard 1970a, Myers et al. 1979a, b). Their behavior offers a striking contrast to that of non-territorial conspecifics moving about nearby in flocks. Does their territorial be-

havior comprise an alternative tactic for reducing predation risk? This might be the case if they are inconspicuous while foraging and if, by spacing out and thereby effecting a lower density, they decrease their predator's foraging effectiveness (Tinbergen et al. 1967, Croze 1970, Curio 1976, Davies 1978). If not and if they defend sites for some other ecological benefit such as foraging efficiency (Gill and Wolf 1975, Charnov et al. 1976), does their behavior compromise their ability to cope with a predator?

In this paper I consider these issues in relation to the Buff-breasted Sandpiper (*Tryngites subruficollis*) on its wintering ground in Argentina. Because almost no information has been published on the wintering ecology of this species (see Myers and Myers 1979), I first examine general features of its non-breeding spacing system. I then address the following points: (a) what is the spatial dispersion of sandpipers when

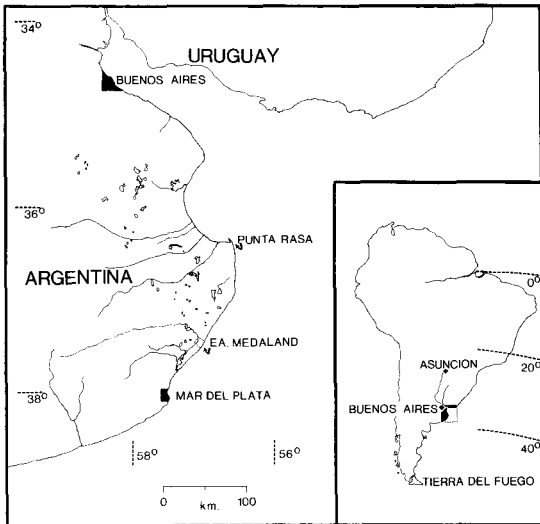


FIGURE 1. Map of the coastal zone of Buenos Aires Province, Argentina, showing the location of the study site, Estancia Medaland. Inset shows the position of this coastal area within South America.

foraging undisturbed; (b) how does their dispersion change with their daily cycle of activity; and (c) how do territorial sandpipers respond to predators?

STUDY AREA

Observations were made on Estancia Medaland, an 11,000-ha ranch located within the coastal zone of Buenos Aires Province, Argentina (Fig. 1). This site, typical of the Argentine pampas near the Atlantic coast, is a mosaic of upland grasslands and seasonally wet marshes. A description of the area and its shorebird community is given by Myers and Myers (1979). Additional information on the region can be found in Hudson (1920), Wetmore (1926, 1927), Weller (1967), Borello (1968), Burgos (1968), and Cabrera (1968).

Data for this study were gathered during two seasons from 15 August 1973 through December 1974. Between 1,000 and 2,000 Buff-breasted Sandpipers used the area during the austral spring and summer of these years. Buff-breasted Sandpipers arrive in coastal Buenos Aires in mid-September (Myers and Myers 1979). They remain on the pampas until late January, when many begin northward migration, yet some can be found as late as March. While in the area, they limit their foraging and territoriality almost exclusively to short-grass uplands where grass is no more than 5 cm high.

Potential predators on sandpipers commonly recorded on the Estancia included the Cinereous Harrier (*Circus cinereus*), Long-winged Harrier (*Circus buffoni*), Crested Caracara (*Polyborus plancus*), and Short-eared Owl (*Asio flammeus*). Peregrine Falcons (*Falco peregrinus*), Barn Owls (*Tyto alba*), and Great-horned Owls (*Bubo virginianus*) were also observed. In addition to these avian predators, a canid (*Dusicyon* sp.) and a felid (*Felis colocolo*) inhabited the ranch. Humans also had a long history of hunting shorebirds here. Around the turn of the century, a canning factory for shorebird meat was located nearby. Recently, however, sandpipers have been protected by law and by international treaty.

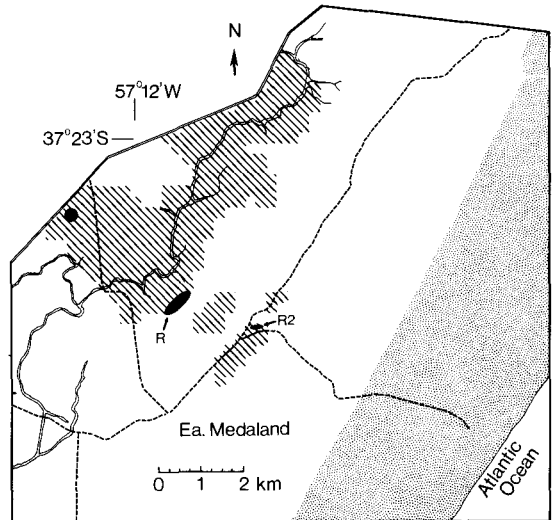


FIGURE 2. Map of the study site, Estancia Medaland, bordered on the northwest by a road and on the southeast by sand dunes (stippling) and the Atlantic Ocean. Diagonal barring shows the distribution of suitable Buff-breasted Sandpiper habitat. The squared pattern is a result of the mapping technique (see text). A black dot identifies the site of the main grid. Large and small black ovals (labeled R and R2) show the positions of the main and secondary roosts used by Buff-breasted Sandpipers.

METHODS

I observed Buff-breasted Sandpipers from elevated blinds adjacent to eight gridded study plots. The most extensive data set was gathered from a blind on the top of a 4-m tower 25 m away from a 75 × 75-m grid (0.56 ha) divided into 25 × 25-m units with permanent stakes. This grid lay within a large expanse of short-grass upland pasture, with the nearest edge of this habitat type (a road, Fig. 2) approximately 250 m away. Buff-breasted Sandpipers foraged throughout the pasture and their behavior on the grid appeared comparable to that observed in adjacent areas.

This plot was watched on six days between 21 October and 28 November 1974. Observations on other plots and general surveys throughout the Estancia spanned austral spring and summer of 1973–74 and austral spring of 1974. Approximately 560 h were spent in field observations during these two years. Data from the intensive observations on the main study grid were analyzed quantitatively to document temporal patterns in sandpiper dispersion using techniques described below. Observations from the other plots provided qualitative supplements to these analyses.

In addition to observations from blinds, I periodically examined all the uplands on the Estancia, usually by car but also on foot or horseback to less accessible sites. The total absence of brush or trees facilitated the survey, as did being able to drive on all the upland habitat. During these surveys I recorded Buff-breasted Sandpiper occurrences on a coordinate system with 250 × 250 m units generated by laying a grid over a 1:50,000 topographic map of the area (Ejercito Argentino Instituto Geografico Militar Hoja 3757-27-2, Faro Querandí). Each unit on the grid was designated as either containing or not containing suitable habitat for this species, with the minimum area of habitat for the former being approximately 0.5 ha. The continuous na-

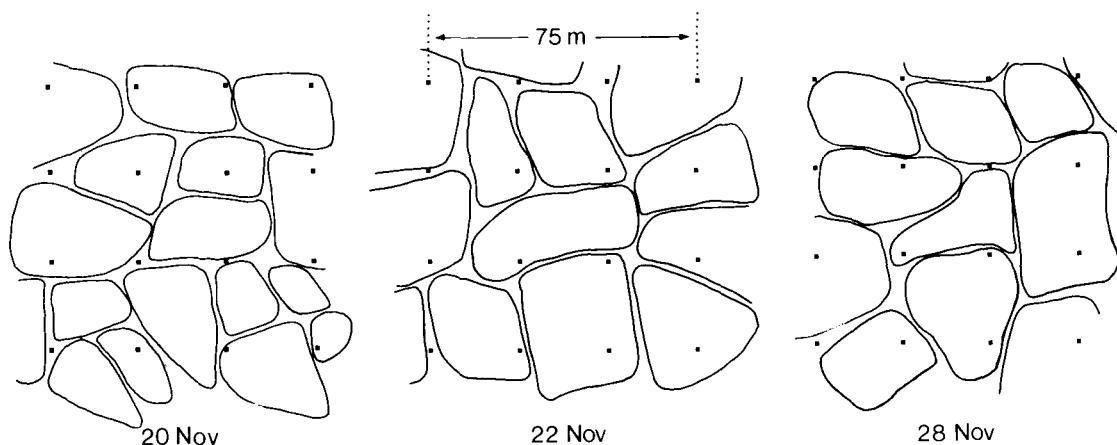


FIGURE 3. The spatial array of Buff-breasted Sandpiper territories defended on the grid on three dates during November 1974. Boundaries are shown with solid lines; small solid squares identify permanent stake positions. Interstices represent areas within which border interactions occurred between neighbors. Non-resident intruders were supplanted from these areas.

ture of the pastures usually meant that if part of the unit was suitable, most or all was. These surveys produced a two-phase mosaic (Pielou 1964) showing the distribution of Buff-breasted Sandpiper habitat (Fig. 2). On these surveys I also recorded interactions between sandpipers that indicated the presence of territorial birds.

By observing evening flight from foraging areas, I located the major roosts used by Buff-breasted Sandpipers on the Estancia. On six evenings between 9 October and 28 November 1974, I tallied flights to the roost from a position along a major flight line from the main study grid within 500 m of the roost. I recorded the number of sandpipers in each flock observed during successive 5-min intervals, beginning 2 h before sunset and continuing until dark. To analyze these data all times were normalized around the moment the sun touched the horizon, which was recorded on each evening of observation.

From the blind adjacent to the main grid, two observers mapped the positions of all shorebirds on the study grid at 15-min intervals throughout an observation session. Birds were easily sighted because of the low and uniform stature of vegetation. After some practice, we were able to plot an individual's position to within 2 m without difficulty. A single mapping normally took less than 30 s. When a flock was present we recorded flock position and size by drawing a rough outline of its perimeter on the map and noting the flock's size within the circle. If a flock spread over more than one grid unit, the numbers of individuals within each unit were recorded separately.

To obtain a quantitative description of sandpiper spacing patterns, from the maps I calculated Lloyd's (1967) index of dispersion \bar{x}^*/\bar{x} , hereafter called D . In this formulation \bar{x} equals the mean number of individuals within each grid unit x_j over the entire grid of n units and

$$\bar{x}^* = \frac{1}{N} \sum_{j=1}^n x_j(x_j - 1).$$

N is the number of individuals present on the entire grid.

Lloyd presented this dispersion index to investigate deviations from random patterns of spacing in mobile animals. Index values less than 1 indicate a tendency

toward even dispersion, while values greater than 1 suggest clumping. The expected value for a randomly distributed population is 1. Several difficulties, discussed below, accompany the use of a dispersion index to define a particular bird dispersion as even, random, or clumped (Lloyd 1967). My study is limited by these difficulties and also by the small number (i.e., 9) of quadrats on the grid. Therefore I use the index only to make relative comparisons among different sampling times, testing whether one set of observations tends to show more clumping than another.

A dispersion index based on nearest-neighbor distances (e.g., Clark and Evans 1954) would have avoided some of these difficulties. The fact that we were not able to map individual positions within a flock (see above) precluded the use of such an index.

RESULTS

TERRITORIALITY

On the Estancia, Buff-breasted Sandpipers defended territories that ranged in size from 0.01 to 0.3 ha per territory. On the main grid 29 territories averaged $0.04 \pm .002$ SE ha. Size, shape, and boundary positions varied among the sampling dates on the main study grid (Fig. 3). While no birds were color-banded, the behavioral consistency of several intensively-watched individuals suggested that at least a few birds remained resident throughout the period indicated by the three dates in Fig. 3. This would be consistent with the behavior of other non-breeding territorial shorebirds (Myers et al. 1979a).

The sandpipers were territorial throughout the Estancia far beyond the limits of the main study grid. During the extensive surveys of upland habitats (see Methods), I obtained records of Buff-breasted Sandpipers in 245 units (Fig. 2). In only 38 of these was there never an indication of territoriality. As

in other non-breeding shorebirds, at any given time not all sites were defended (Myers et al. 1979a). Yet at times Buff-breasted Sandpiper territoriality was very widespread over areas used by the sandpipers on the Estancia. This was particularly true in November 1974, when territorial individuals could be found throughout the Estancia's short-grass uplands.

The sandpipers used a few simple displays in territorial defense. Chasing often began with the resident raising one wing vertically as it ran toward an intruder, revealing the wing's marbled undersurface. This display was also given by stationary birds to potential intruders flying low over the territory. Oring (1964), Previtt and Barr (1976) and Myers (1979) described the wing-up posture in Buff-breasted Sandpipers (Oring's 1A display) on migration stopovers and on breeding grounds.

Interactions with neighboring territorial birds often entailed erecting backfeathers and depressing the tail while moving slowly near their mutual boundary. Neighbors frequently crouched together at the boundary for several minutes, oriented parallel to one another and the boundary line and separated by less than 20 cm. These displays closely resembled postures used by other calidridine sandpipers on non-breeding territories (Hamilton 1959, Myers et al. 1979a).

When neighbors or non-territorial birds trespassed upon a territory, the response was immediate: the resident ran or flew toward the intruder and chased until the intruder left. These supplantations occurred over the entire width of a territory, and chases occasionally began with the intruders at the opposite side of the territory, as far as 75 m away.

I collected three individuals on their territories to determine if either sex defended sites. Two were male and one was female. All three lacked a bursa of Fabricius and were therefore more than one year old (McNeil and Burton 1972). That females could be territorial was also indicated by the fact that territoriality continued through March even though males left the area by early February: of 23 sandpipers collected between September and January, 17 were male, while of the 11 collected in February and March all were females.

THE DAILY CYCLE

Buff-breasted Sandpipers reached their foraging areas each morning shortly after sunrise. They often arrived at the main grid in flocks of 5 to 20, flying from a roost approx-

imately 3.5 km distant (Fig. 2). Upon arrival, the compact flocks normally dispersed quickly, with individuals going directly to their foraging territories. Unless disturbed, each bird usually remained foraging on its territory throughout the morning and early afternoon hours. In mid-afternoon birds left their territories and flew to nearby water for bathing and drinking. These flights usually occurred in flocks, so that often the entire local contingent of sandpipers abandoned the area around the grid. They were accompanied to the water by locally feeding (and territorial) American Golden Plovers (*Pluvialis dominica*). Each individual's absence from its territory lasted from 20 min to one hour. Territory holders returned in flocks and again went to their territories. Their persistence of defense, however, appeared to wane during late afternoon. Birds seemed to react more slowly to intruders and they more readily joined others in small foraging flocks.

This laxness in defense continued toward early evening. On rare but regular occasions, all semblance of a territorial array broke down when groups of 10 to 50 birds congregated into small (less than 0.01 ha) areas. Within these groups, individuals displayed actively toward one another; several birds would simultaneously present an open-wing display (2C in Oring 1964) or begin flutter-jumping (Pitelka et al. 1974). None remained still within the area. Comparable use of breeding displays on the wintering ground throughout the non-breeding season has been observed in no other shorebird species and may relate to the unusual breeding pattern of this species (Pitelka et al. 1974, Myers 1979).

I never saw such groups form twice in the same location. None occurred on the study grid itself during my observations, but they did form on areas nearby that had been defended earlier in the day.

Buff-breasted Sandpipers moved to their roosts in flocks (Fig. 4). The average flock size in roosting flights was six birds (n of flocks = 430). However, this value, heavily influenced by flocks of small size, gives a misleading impression of the flock size experienced by the average bird. Most birds, in fact, traveled in groups of 5 to 20 (Fig. 4) and the average bird flew with 16 others per flock. This value represents the mean number of birds per bird in a flock, calculated as Lloyd's (1967) mean crowding index, \bar{x} (see Methods).

In the evening, roosting flights commenced one h before sundown and peaked

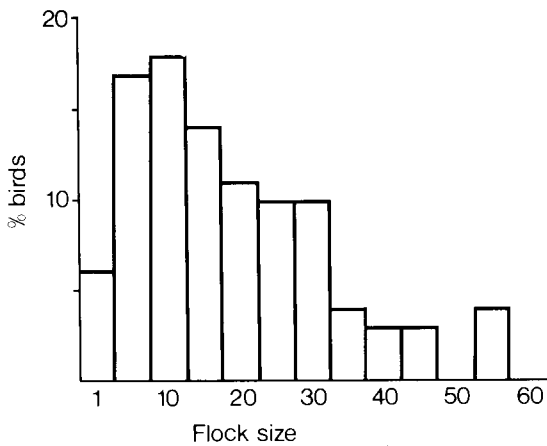


FIGURE 4. The percentage of Buff-breasted Sandpipers moving to their roosts in flocks of different sizes.

approximately 40 min later (Fig. 5). Movements ended by sunset. Buff-breasted Sandpiper flights occurred markedly earlier than those of other local shorebird species, even those foraging in the same habitats such as American Golden Plovers (Fig. 5).

On the Estancia, Most Buff-breasted Sandpipers roosted together in one flock at the edge of a short-grass pasture bordered by a marsh (Fig. 2). I regularly observed sandpipers from the main study grid fly directly to this area, where they joined others arriving from locations throughout the Estancia. Before settling down for the evening, the accumulating flock often whirled for 5 to 10 min over a 500 × 300 m area. The precise site of the roost fluctuated within this area among different nights. I estimated that 600 to 1,000 Buff-breasted Sandpipers used this roost. Up to 100 used a secondary roost nearby (Fig. 2). Examining the roosts at night by night-light, I found individuals tucked in small depressions in the grasses or behind grass tufts, usually no closer than 20 cm from another bird.

Of the 11 other common non-breeding shorebirds present on the Estancia in austral spring and summer, only the Two-banded Plover (*Charadrius falklandicus*) also roosted in monospecific flocks. All other species roosted in large monospecific aggregations, usually in a flooded wetland. The locations of these roosts were less variable than that of the Buff-breasted Sandpipers.

DISPERSION ON THE FORAGING AREA

Temporal changes in Buff-breasted Sandpiper dispersion during undisturbed periods are shown in Figure 6. Time of day had no significant effect on dispersion

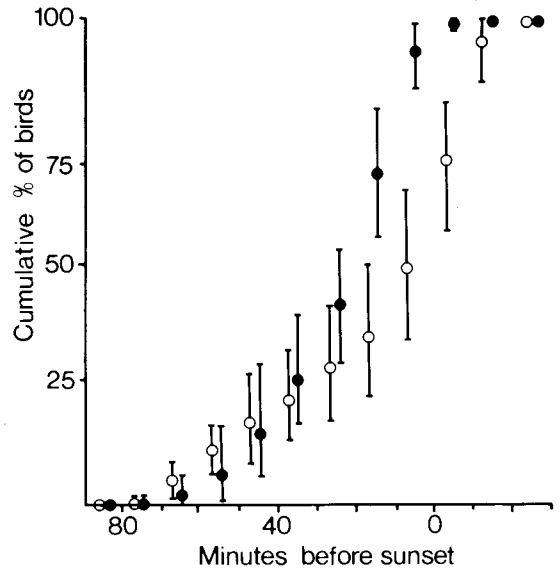


FIGURE 5. The timing of movement to roosts. Mean and 95% confidence interval for the cumulative proportion of individuals that had flown to the roost by a given time before sunset. Closed circles, Buff-breasted Sandpipers. Open circles, American Golden Plovers.

(Kruskal-Wallis nonparametric one-way ANOVA, $\chi^2 = 17.0$, $P > .11$). While the trends are not statistically significant, the daily pattern of dispersion appears to follow the qualitative features of the daily cycle of territorial occupancy as described above. Mean values are higher and confidence limits are broader early in the morning when the birds arrive than in late afternoon when defense becomes more lax. This is supported by the non-homogeneity of variance of dispersion among different times of day (Bartlett's $F = 6.5$, $P < .001$).

The mean density and 95% confidence interval for all maps of birds foraging undisturbed on the grid was 0.99 ± 0.05 birds per grid unit or 16 birds per ha. Mean and confidence limits for the dispersion index was 1.13 ± 0.15 . This suggests a statistically random dispersion, but several factors, discussed below, complicate this interpretation. The dispersion index was not correlated significantly with density ($r = -0.10$, $P > .10$, $n = 152$).

THE RESPONSE TO PREDATORS

In two seasons' observations (approximately 560 field hours) I saw no predation attempts on Buff-breasted Sandpipers, although I did witness predation on another local shorebird species, the Southern Lapwing (*Vanelus chilensis*) by a Crested Caracara (Myers 1978). Nevertheless, the response of resident sandpipers to a predator's appearance

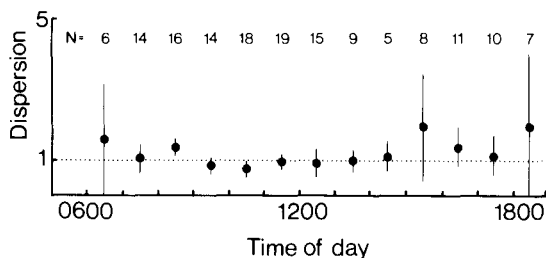


FIGURE 6. The daily pattern in dispersion of Buff-breasted Sandpipers on the main study grid. Mean and 95% confidence interval of Lloyd's (1967) dispersion index is plotted for each hour. Dotted line identifies the expected $D (=1)$ for a random distribution. Higher values indicate relatively greater degrees of clumping. Sample size given above each mean.

was consistent: they abandoned their territories and joined together in a flock, whirling over the foraging area in flight. I often could tell that a predator was approaching because it set off a wave of American Golden Plover alarm calls rolling over the grasslands. Although the Buff-breasted Sandpipers were silent, they flew with the plovers. Once the predator disappeared, they usually landed together and quickly returned to their territories.

A typical sequence is shown in Fig. 7. Before the predator appeared, birds were dispersed evenly on their territories. Immediately upon the predator's approach they flew up, joined a flock in the air, and circled the area briefly. As the predator departed they landed on the grid and dispersed to their territories. As indicated in the figure, they usually recovered quickly from the disturbance.

To examine the effect of a predator on dispersion I compared maps made immediately prior to the predator's approach (i.e., the last one immediately before appearance; up to 15 min before) with those taken immediately afterward (within 4 min). For any given appearance, I used only one measurement from before and one from after.

The results are summarized in Table 1. If birds landed on the grid within 4 min of a disturbance by a predator, grid density was higher than it had been before the predator appeared (ANOVA, $F_{1,34} = 4.24$, $P < .05$). Therefore, to test for differences in dispersion, I used an analysis of covariance because D is potentially sensitive to density over a broad range of densities. The main treatment (appearance of a predator) and the covariate (density) were entered simultaneously using a regression design (Nie et al. 1975). The results show that birds were

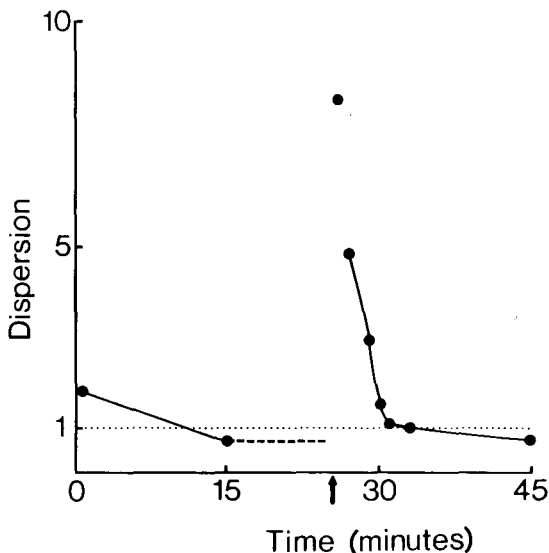


FIGURE 7. Changes in Buff-breasted Sandpiper dispersion after the appearance of a predator (Swainson's Hawk, *Buteo swainsoni*) at the arrow. Ordinate is Lloyd's (1967) dispersion index. Higher values indicate greater degrees of clumping. Solid line connects the samples between which sandpipers did not fly. Dashed line shows the estimated dispersion between the last sample and the moment the predator flew over. Dotted line identifies the D expected for a random distribution.

significantly more clumped after a predator appeared ($F = 26.1$, $P < .001$), but that density did not contribute to the effect ($F = 0.01$, $P > .88$).

Infrequently an individual bird on the grid would not fly with the rest of the birds. Instead, it remained crouched on its territory, pressed to the ground. After the predator disappeared it resumed foraging within a few minutes.

DISCUSSION

While the dispersion data corroborate the qualitative observations, the information must be interpreted cautiously because of several methodological difficulties. I discuss them here because of their importance for this study and also because of their rel-

TABLE 1. Mean density and mean dispersion before and after the appearance of a predator^a.

	Before	After
Density (birds/unit)	1.0 ± 0.1	1.7 ± 0.6
Dispersion (D)	0.9 ± 0.2	4.3 ± 1.1
No. observations ^b	16	20

^a 95% confidence limits for means included.

^b Numbers before and after differ because on four occasions birds were not present on the grid at the regular sampling time even though they did return before the predator appeared.

evance to using dispersion indices for studying bird spacing patterns in general. The first problem concerns the heterogeneous nature of the sandpipers' distribution. Local populations of wintering shorebirds are a mixture of individuals using different spacing behaviors (Recher and Recher 1969, Goss-Custard 1970a, Myers et al. 1979a, Pitelka et al. 1979). Thus it is possible that no single statistical distribution will adequately describe the spatial pattern in a particular set of wintering shorebirds. For example, in some cases small flocks of non-territorial Buff-breasted Sandpipers entered a grid dominated by territorial birds. While the territorial birds alone should have produced an even pattern and the flocking birds alone an aggregated one, combining both as if in a single distribution yielded an overall mean D near 1, the random expectation. Thus combining both space-use patterns in a single distribution makes testing for deviations from randomness per se both statistically and biologically misleading.

It is intriguing, nevertheless, that in these observations the heterogeneity in sandpiper behavior simulated an apparently random distribution, especially in light of the review by Taylor et al. (1978) of the frequency of different dispersion patterns in animal populations. Random distributions are rare.

These two points—the pseudo-random distribution in Buff-breasted Sandpipers and the rarity of randomness in animals in general—caution against accepting Stinson's (1980) attempt to test the importance of predation in the formation of shorebird flocks. He predicted that if predation is important, then shorebirds should not be distributed randomly. The present work suggests that even when an apparently random distribution is found, it may not result from homogeneous behavior.

A second problem arises when assumptions are made about the underlying distributions of habitat or resources. When these distributions are uniform, the expected bird distribution based on an assumption of randomness with respect to other birds can be calculated readily. But it becomes difficult to specify the expected distribution if prey are distributed unevenly and birds respond to local variations in resource density (e.g., Goss-Custard 1970b, Zach and Falls 1976, Myers et al., 1979b). This difficulty, nonetheless, does not obviate relative comparisons among patterns if the resource distributions remain constant. In the present study it is highly improbable that changes in

either resources or habitat produced the observed changes in dispersion. Matching each predator-disturbed measurement with the immediately preceding undisturbed measurement shows that in every case ($n = 16$) the disturbed dispersion index is higher (sign test, $P < .05$). Yet matched pairs were taken less than 19 min apart at most in a flat, uniform short-grass field.

A third problem concerns the sensitivity of dispersion indices to quadrat size and to bird density. Quadrats must be small relative to patch size, and further, they must be small enough so that the mean density of animals per quadrat is relatively low (i.e., so that the animal is relatively rare; Lloyd 1967). In theory, when these assumptions (and those above) are met, then a random distribution should have a D value of 1 (Lloyd 1967). When these assumptions are grossly violated, the D value expected for a random distribution becomes difficult to specify. In my study I knew something of the range of territory sizes defended by Buff-breasted Sandpipers and selected a 25-m \times 25-m quadrat size accordingly. I also examined the effect on dispersion of the range of densities measured on the grid in order to ensure that changes in density alone were not responsible for the measured changes in dispersion.

COMMUNAL ROOSTING AND TERRITORIALITY

Buff-breasted Sandpipers move to and from their foraging areas in flocks. They roost communally, yet while feeding, they often defend territories. This combination of refuging (Hamilton and Watt 1970) with foraging area territoriality is common among wintering shorebirds (Myers and Myers 1979, Myers et al. 1979a), but among mobile animals in general it may be an unusual pattern (Lack 1968, Brown and Orians 1970, Wilson 1975). It has been reported in a few other taxa, including wagtails (Davies 1976), herons (J. A. Wiens, unpubl. data), terns (J. J. Hatch, unpubl. data), and bats (Bradbury and Vehrencamp 1976).

Foraging area territoriality implies some faithfulness to the defended site through time. In other species of sandpipers behaving like these Buff-breasted Sandpipers, banded individuals defended sites for long periods, often over a month and occasionally more than 100 days (Myers and Myers 1979, Myers et al. 1979a). Although none of these Buff-breasted Sandpipers was banded, their behavior suggested that individuals returned repeatedly to the same site.

The combination of refuging and feeding

area territoriality seen here would appear to contradict interpretations of refuging or communal roosting based on information transfer (e.g., Zahavi 1971, Ward and Zahavi 1973, Krebs 1974). No studies of this hypothesis have carefully assessed the faithfulness of individuals to different foraging areas. A central tenet is that individuals do switch from site to site, their movements influenced by information transferred within the roost. If many do not switch, then the argument is weakened. It can be salvaged in the shorebird example by maintaining that individuals use territories normally but they benefit from roosting together because of rare but recurring occasions when resource distributions change abruptly. More study is necessary on the foraging locations of known individuals and the events leading to their site changes.

TERRITORIALITY, FLOCKING, AND PREDATION

Buff-breasted Sandpiper activities vary through the day. Whenever a predator approaches, territorial sandpipers behave as do non-territorial shorebirds in similar situations (Lack 1968, Goss-Custard 1970a, Page and Whitacre 1975): they join together while the predator remains nearby and afterward return to their territories.

This study provides no direct evidence for the hypothesis that shorebirds reduce their risk to predators by being in a flock. The consistency in timing and form of the response to predators nevertheless indicates that by joining a flock territorial Buff-breasted Sandpipers somehow benefit. Since they flock after a predator appears, the benefit cannot be from predator detection, that is, from having more eyes present to detect a predator more rapidly or reliably (Lack 1968, Powell 1974). Rather, the benefit probably relates to lowering the likelihood of attack or to reducing the risk during attack, either by decreasing the attack success rate or by spreading the risk to other flockmates.

Goss-Custard (1970a) proposed that in shorebirds, interspecific differences in dispersion patterns result from interspecific differences in the costs of flocking due to feeding interference with conspecifics, combined with benefits from flocking because of predation. Species with greater interference should accept higher predation risks because the costs of flock foraging are higher. As a result, these species should be more evenly dispersed. Interpreted within this framework, my results suggest that

Buff-breasted Sandpipers either face strong feeding interference, light predation on the study area, or both. While the time and energy expended in territorial defense supports the first possibility (Myers et al. 1979a), the fact that predators appeared infrequently and that none actually attacked lends credence to the latter.

My results also imply that territoriality in Buff-breasted Sandpipers apparently does not relate to reducing individual risk from predation, although this may be important in other predator-prey systems (Tinbergen et al. 1967, Sherman 1976, Davies 1978). On the contrary, these sandpipers leave their territories once a predator appears. Nevertheless, one benefit of territoriality in relation to predation may exist. By reducing their local density through aggressive spacing, the sandpipers might make their sites less attractive to a predator. In doing so, they might decrease their risk because the predator, responding to prey density, would spend more time elsewhere. Territoriality would thereby function as an early defense line in a hierarchy of anti-predator behaviors, with the second stage being flock formation once the predator appeared. Each stage would focus on different components of the predation sequence, from locating areas of high profitability for foraging to prey capture and handling.

Other facts, however, argue against this interpretation. In particular, were this the case, then sandpipers should be territorial against all individuals with whom they share predators, including other shorebird species (Myers et al. 1979a). On my study site, American Golden Plovers and Buff-breasted Sandpipers defended territories which overlapped completely. Neither species showed interspecific territoriality, nor did other pairs of shorebirds defending non-breeding territories syntopically. These pairs included Pectoral Sandpipers (*Calidris melanotos*) versus White-rumped Sandpipers (*Calidris fuscicollis*), and White-rumped Sandpipers versus Two-banded Plovers (Myers and Myers 1979).

A third issue raised by these findings is the effect that predation intensity may have on territorial behavior. Because predators disrupt the sandpipers' territorial arrays, shorebirds may be less likely to defend territories in places where predators appear frequently. Following disruption by a predator, time and energy must be spent in reasserting territorial residency and evicting intruders.

A final implication of these findings con-

cerns the relationship between flocking and territoriality, which are often viewed as opposite extremes on a continuum (e.g., Brown and Orians 1970). While Buff-breasted Sandpipers forage territorially, they effectively remain within a flock, albeit a loose one. Whether the local spatial dispersion is even or clumped may be immaterial to the question of flocking, at least with regard to their participation in flock activities. What matters here is that under appropriate environmental circumstances the behavior of local residents becomes linked and cohesive. In essence, they are always within a flock. They can maintain both behaviors at once because each addresses different requirements, feeding versus predator avoidance. Local habitat features (high visibility), small territory size, and evolutionary history (in the sense that flocking is a common shorebird pattern) probably abet the duality. The continuum in spacing behavior suggested by Brown and Orians (1970) actually exists in two (or more?) dimensions. A bird must choose whether or not to defend, and simultaneously, to what extent it should associate with other individuals.

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RECENT PUBLICATIONS

Indian Hill Birds.—Salim Ali. 1979. Oxford University Press, New York. 188 p. \$24.95. This is virtually a reprint of the book originally published in 1949. A new preface gives the territorial names which have been changed since then. A pocket-size field guide, it describes in some detail the birds of the Indian hills—Himalayan as well as peninsular. The accounts cover size, field characters, distribution, habits, and nesting. The order of species is that of the earlier time (corvids to partridges), but there is an index. The book includes endpaper maps, color plates by G. M. Henry, photographs, a distribution chart, and a key for field identification. Birders in the Himalayas should compare this work with the same author's recent field guide to the birds of that region (noticed in *Condor* 80:457) to see which will serve them better.

Birds of the Labrador Peninsula and adjacent areas/A distributional list.—W.E. Clyde Todd. 1980. Buteo Books. 822 p. \$70.00. This major avifaunal study was first published in 1963 by the University of Toronto Press in association with the Carnegie Museum. For an appraisal of it, see the special review by Oliver Austin (1964. *Auk* 81:461-464). The book has now been reissued with the addition of four pages, including material on the author and a list of additions and corrections. The new pages are available separately on request, for a \$1.00 handling fee from Buteo Books, P.O. Box 481, Vermillion, SD 57069.