

Figure 1. Map of the 3000 hectare North Inlet marsh.

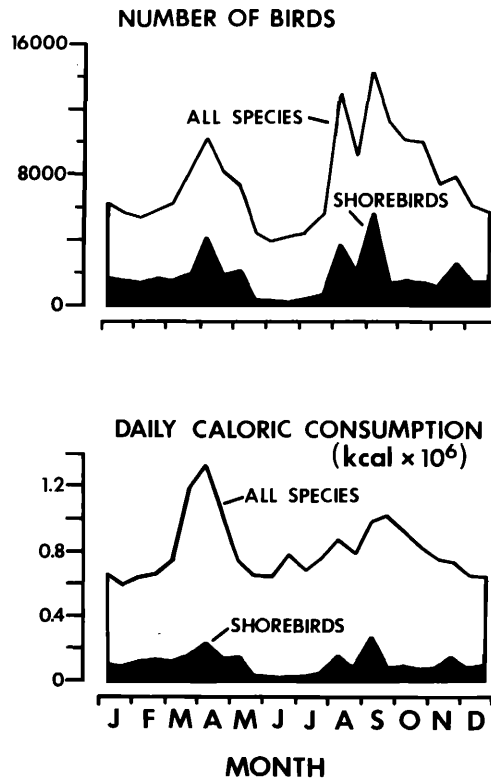


Figure 2. Seasonal fluctuations in the number of birds and in avian induced energy flow on the North Inlet marsh. Shorebird contributions are indicated in black.

Table 3. Seasonal and annual summaries of shorebird numbers, biomass, and caloric consumption.

	Number of individuals	Biomass (kg wet weight)	Caloric Consumption (kcal x 10 <sup>3</sup> /day)
Winter	1605(28) <sup>a</sup>	212(12)	117(17)
Spring	2082(27)	263(10)	140(14)
Summer	1759(21)	216(9)	90(11)
Fall	1605(20)	212(11)	103(14)
Annual Mean	1765(23)	224(10)	109(13)

<sup>a</sup>Percent of avian community

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TERRITORIALITY OF WHIMBRELS *NUMENIUS PHAEOPUS HUDSONICUS* WINTERING IN PANAMA

by Elizabeth P. Mallory

Several workers have concluded that behavioral and ecological differences between closely related and/or ecologically similar shorebirds on the wintering grounds have evolved to minimize competition among migratory species, or between migratory and resident species (Ashmole 1970; Baker & Baker 1973). Marked geographic isolation has been found among ecologically similar migrants, or migrants and residents (Myers 1980a), and this pattern probably evolved as a response to competitive pressures in the past.

Interspecific aggression and territoriality among organisms indicates the existence of competition without sufficient evolutionary divergence to provide ecological isolation. Recently, several studies have shown intraspecific territoriality to be widespread in wintering migrant shorebirds (Myers et al. 1979a, 1979b, 1981; Myers 1980a, 1980b). Although winter territoriality is labile in one species studied in north temperate latitudes (Myers et al. 1979a), this is at least in part a response to fluctuating food resource levels (Myers et al. 1979b) and intruder densities (Myers et al. 1981). In species wintering in tropical and austral regions, territoriality can be relatively stable and persistent (Myers 1980a, 1980b; this study), although in many it still shows variability comparable to north temperate systems (Myers & Myers 1979). Also, site tenacity by returning migrant shorebirds indicates that their affiliation to the wintering ground is equivalent to that of the breeding grounds (Middlemiss 1962, Moreau 1972, Elliot et al. 1976, Smith & Stiles 1979).

From January through March 1979 I studied the foraging ecology of wintering Whimbrels *Numenius phaeopus hudsonicus* on an intertidal area in the mouth of the Panama Canal (8°57'N, 79°34'10"W; Figure 1). At the time of the study, this area was within the Canal Zone, somewhat protected from human disturbance. This site was located northwest of the Pan American Highway bridge crossing the canal, and was composed mostly of silty, soft mud bordering a stream channel down the middle, sandier areas on both sides, and a landward margin of mangroves.

Each day the tidal cycle becomes about 45 to 60 minutes later, following the normal pattern of slightly less than two cycles per day. The tide ranges from 3 to 5 meters between neap and spring tides, on the two week cycle. During more extreme (spring) tides, areas are exposed faster and longer, total exposure is more extensive, and then flooding is more rapid. The tidal pattern determines the time available to shorebirds for feeding, and could be important if foraging time is a limiting factor.

The frequent occurrence of agonistic encounters during my study of foraging behavior in wintering Whimbrels (Mallory 1981) led me to suspect that Whimbrels had feeding territories on the mudflats. To confirm territoriality I staked out the mudflat with a 50 m grid. I then mapped movements of individual Whimbrels over time. I followed several individuals simultaneously, marking their locations at 5 minute intervals and drawing lines along the birds' paths between those points. I recorded all agonistic encounters between neighbors.

Territorial agonistic encounters exhibit a range of intensity. The most intense entails actual physical contact where the Whimbrels, especially the attackers, jab or bite each other with the bill. Usually the encounters involve ritualized fighting and avoidance of physical contact. An aggressive Whimbrel struts about in erect posture, feathers puffed, calling frequently facing the other head on, and flashing the undersides of its wings. During a standoff between two Whimbrels, both often exhibit displacement pecking at debris on the flat, and/or, in aggressive postures, run along together parallel to the border of their territories, and/or, escalate to physical contact. Eventually one Whimbrel turns its back to the other, and with compressed plumage and low profile slowly walks away. The other may chase briefly or stand and watch it. Frequently, the encounter is one-sided from the start, with one bird clearly on the offensive, chasing out an intruder from an area the former normally frequents. In these cases, the chaser often returns to forage in the area of the initial encounter. The least intense encounters are supplantings, where the intruder flees before the attacker reaches the intruder.

I overlaid maps made in the same areas on eight days (average of 4.75 days from any one place) over a 7 week period, to produce a composite of all the time interval locations based on 23.57 hours of observation. I felt that the overlapping of maps from successive days was valid for two reasons. First, successive maps show very similar patterns and matched very well. Second, the one color-banded bird and another distinctively plumaged bird were at the same locations every day that I looked for them between early February and mid March.

I used the composite for my complete study area of 12.5 ha to draw territorial boundaries, with agonistic encounters marking the borders (Figure 2). Territories ranged from 0.15 to 1.07 ha ( $\bar{x} = 0.63$ , S.D. = 0.31). The small territory was unusual and not permanent. Its occupant was there only 2 days, and it had inserted itself through considerable aggression into an area where 4 or 5 territories came together. Such an area may be prone to confusion regarding ownership, since so many neighbors come into contact there, and this may have allowed the interloper a temporary and precarious foot-hold.

The territories were defended mostly against conspecifics. Individuals of other species of shorebirds, herons, ibises, and passerines in almost every case were allowed to forage unmolested. Of 60 encounters recorded during the mapping sessions, 57 were directed at other Whimbrels (95%), 2 were directed at Wilson's Plover *Charadrius wilsonia* (3%) and one at a Willet *Catoptrophorus semipalmatus* (2%). However, both the latter species were usually tolerated within Whimbrel territories. For example, individuals of both species were present within Whimbrel territories when I mapped their movements (1.1 hr for Wilson's Plover and 5.05 hr for Willet).

Winter territoriality by Whimbrels suggests that intraspecific competition may be important in Panama. The density of territorial Whimbrels in Panama was 1.10 birds/ha. This is about ten times higher than that found by Skeel (1976) in the breeding grounds (0.11/ha in 1973, 0.10/ha in 1974). Skeel (1976) argued that Whimbrel breeding territoriality was not primarily for defense of food, but rather for protection against nest predation. Myers (1980b) found the territories defended by shorebirds wintering in Argentina's inland Pampas habitat to be ten to one hundred times more dense than those found in the breeding season. He concluded that those winter densities reflect "heavy intraspecific competition for food". The winter feeding territories in Panama are the only cases I observed of Whimbrels defending food resources in a study of the species at breeding, fall migratory and wintering areas (Mallory 1981).

Winter territories in the study area differ in size, depending on substrate characteristics (Figure 2). Significantly ( $t_{10} = 5.893$ ,  $P = 0.0002$ ) larger territories occurred where the substrate was firm, dried considerably with exposure, and was composed of sand and shell fragments (mean 0.984 ha, S.D. 0.139,  $n = 5$ ). Smaller territories occurred where the substrate was soft, always saturated, and composed of silt or mud (mean 0.485 ha, S.D. 0.172,  $n = 9$ ). This non-uniform spacing of birds argues against territoriality functioning only to space the birds out in defense against aerial predators. Also, when a predator is nearby, Whimbrels usually desert their territories (see also Myers 1980a).

I predicted that the smaller territories in mud had been placed in areas of greater crab density. Samples taken within a 10 cm diameter core confirmed this prediction: mean number of crabs in 17 cores on sand was 0.24 (S.D. 0.56), compared with 1.3 (S.D. 1.72) in 15 on mud (Mann-Whitney  $U = 273.46$ ,  $P = 0.001$ ). The crab fauna at these sites belonged to at least four families, Xanthidae (mud crabs), Portunidae (swimming crabs), Pinnotheridae (pea crabs) and Ocypodidae (ghost crabs); and there probably are differences, although undocumented, among them in preference for sandy or muddy habitats. Therefore, the different crab densities may be a result of different species composition. I was unable to obtain Whimbrel gut contents to see which crab species they actually were eating, although observation suggests that oscypodids and xanthids were the most important.

I further predicted that if more food resources enable (or force, due to competition) Whimbrels in muddy areas to have smaller territories, then there should be some direct effect on their foraging rates or success. I observed Whimbrels in sandy and muddy areas for 96 three minute samples to compare their foraging rates and success (Table 1). Individuals in sandier areas (larger territories) foraged at a faster rate but had equivalent success to Whimbrels foraging in muddy areas (smaller territories).

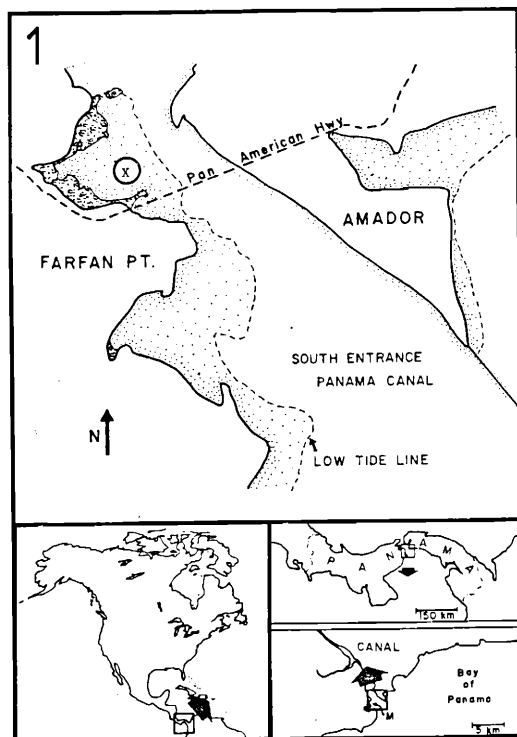


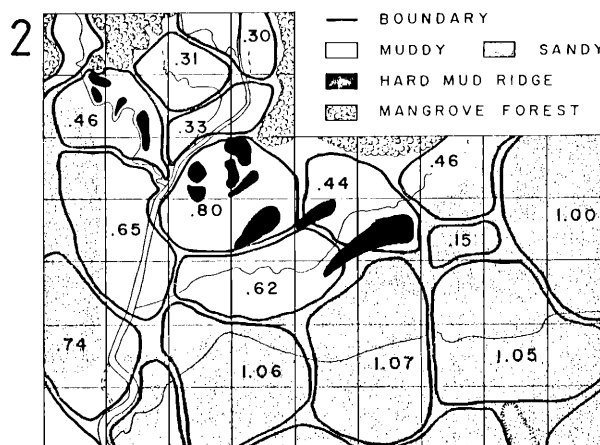
Figure 1. Location of the study area in the Pacific mouth of the Panama Canal. The X marks the study site.

Figure 2. Map of Whimbrel winter feeding territories showing sizes (ha) and substrate types. Four sections of the 50 m grid equals one hectare.

Table 1. Whimbrel foraging rates and percent success in territories with sandy or muddy substrates.

		Substrate	
		Sandy	Muddy
No. of attempts per 3 minutes sample	$\bar{x}$	56.3	42.9
	S.D.	24.6	20.2
	N	53	43
Percent success	$\bar{x}$	11.4	12.7
	S.D.	1.1	1.8
	N	53	43

Foraging rates t-ratio = 2.8829 on 94 df; P = 0.0049  
 Percent success t-ratio = -0.88906 on 94 df; P = 0.379



Smaller territories may not reflect increased prey density but rather increased competition from intruders, as Myers et al. (1981) found for Sanderlings *Calidris alba*. It is difficult to tease apart these two alternatives using my data, but the stability of Whimbrel territorial arrays implies that a basic tenet of Myers et al.'s model for Sanderling territoriality may not be applicable: the model they present (Myers et al. 1981, Fig. 7, 1-C) assumes that Sanderlings cannot track optimal territory size because of variable and unpredictable food resources. Whimbrels are morphologically and behaviorally adapted to a specialized subset of invertebrates in their feeding habitat (Mallory 1981). For Whimbrels, the availability of crabs did not seem to diminish, and there was more or less constant level in numbers of all other potential prey during the same period one year before this study (Schneider 1978, Mallory 1981). Thus, it is conceivable that Whimbrels could track optimal territory size. Their territoriality may be represented by a version of the Myers et al. (1981) model that is sensitive to prey density (their Fig. 7-1D). Resolving this issue, however, will be complicated, since defenses, life history strategies, and predictability of prey must each have a profound effect on predator resource utilization, and consequently, on the territorial behavior of Whimbrels.

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