

A review of territoriality in non-breeding shorebirds (Charadrii)

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I reviewed species accounts and the primary literature for 215 shorebirds to provide an up-dated review of the occurrence of territoriality during the non-breeding season. In total, 52 species have been recorded defending territories. From the primary literature, I found 78 reports of territoriality in 42 species, most of which were plovers and lapwings (n = 14), calidridine sandpipers (n = 11), tringine sandpipers (n = 11), and curlews (n = 4); it has also been reported in ten other species. Among higher taxa, territoriality is most prevalent in tringine (65% of species) and calidridine (46%) sandpipers. Territoriality occurs regularly in some species (e.g., *Numenius spp.*, *Pluvialis spp.*), whereas it has not been reported or does not occur in 163 species. Of 69 published accounts in the primary literature, most (69%) were from latitudes greater than 30° north (43%) and south (26%), but this may be attributable to sampling effort. Duration of defence varied from hours to months (e.g., *Calidris alba*); individuals of some species returned annually to the same territory (e.g., *Pluvialis squatarola*, *Numenius arquata*) or were resident year-round (e.g., *Haematopus bachmani*). Size of territories varied from a few metres along river shores (e.g., *Tringa glareola*) to several hectares (e.g., *Numenius*); larger species tended to defend larger territories. Territoriality occurs mostly in species that detect prey visually.

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INTRODUCTION

The occurrence of territoriality in non-breeding shorebirds has long drawn the attention of ornithologists (e.g., Michael 1935; Hamilton 1959; Panov 1963; Recher & Recher 1969). Approximately twenty years ago, this interest culminated in several papers in which Myers and his colleagues (Myers *et al.* 1979; Myers & McCaffery 1984; Myers 1984) reviewed the occurrence of territoriality and ecological conditions influencing its behavioural expression. Since then, considerable research has shed additional light on the occurrence of territoriality in migrating and wintering shorebirds. The purpose of this paper is to provide a current review of the extent of territoriality in non-breeding shorebirds. For a thorough treatment of the ecological conditions favoring defence of a food-based territory, see reviews by Myers *et al.* (1979), Myers (1984), and Goss-Custard (1985).

METHODS

Sources

I reviewed three sources (Cramp *et al.* 1983; del Hoya 1996; and the Birds of North America species accounts) providing species accounts of the 215 shorebirds of the world. From these references and an independent literature review, I identified original papers describing territoriality for shorebird species (see Table 1 for scientific names).

Definitions

For this review, I defined territoriality as defence of a fixed location by an individual for a variable duration (see Wittenberger 1981 for a review of definitions). For non-breeding shorebirds, territory defence was nearly always associated with a food resource. Exceptions included species in which individuals remained on territories year-round, which made it difficult to distinguish between defence of a breeding site vs. defence of food resources. Nevertheless, I included these species as territorial during the non-breeding season. I was conservative in what I consider to be evidence for territoriality. For example, Ashmole (1970) mentioned that spotted sandpipers *Actitis macularia* "were solitary feeders and were hostile to members of their own and other species". This strongly suggests territorial behaviour. Nevertheless, unless the author specifically mentioned territoriality or a relationship between food-based aggression and defence of a location, I did not record this as such. Usually (such as spotted sandpipers above), however, other accounts confirmed territoriality.

In reviewing original papers, I summarized location by providing latitude and longitude of the study area; otherwise I listed the general locale. Territoriality varied widely in its timing and duration. Hence, I noted the season (year-round, winter, or months) in which territoriality occurred and duration of defence as lasting



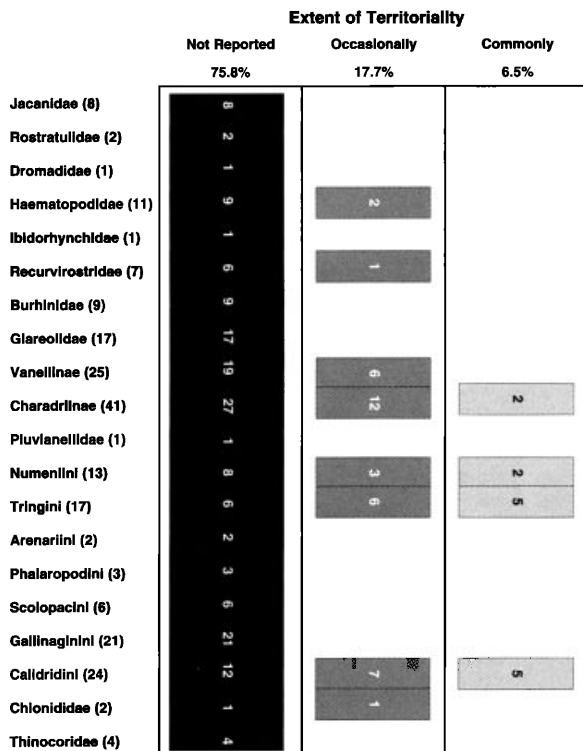


Figure 1. Taxonomic distribution of territoriality in 215 shorebird species.

hours, days, months or years. Territoriality occurred in a variety of marine, freshwater and terrestrial habitats, which I categorized according to the principal habitat description provided by authors. Marine habitats included rocky shores, ocean beaches, protected intertidal flats and channels of bays, estuaries and mangrove lagoons, all of which had varied substrate types. Non-marine aquatic habitats included freshwater ponds, salt ponds, sewage ponds, and river shoreline. Lastly, terrestrial habitats included pastures, mowed lawns and airfield runways. Usually, I reported territory size in area (ha). However, for species that defended stretches of beach or shoreline, I reported territory size in linear distance (m). Occasionally, papers summarized work on marked birds; hence, data were sometimes available on individual sex and age. Lastly, I noted the principal prey associated with territory defence, and other relevant comments of authors.

For each of the 215 species (see del Hoya 1996), I categorized territoriality as *not reported* if none of the species' accounts or primary literature mentioned food-based defence of space. In many cases, these accounts described taxa as "gregarious" or "occurring in flocks" of varying size, which suggested an absence of territoriality. Hence, the summary is conservative in that it assumes territoriality does not occur if it has not

been reported. Conversely, I noted when accounts described species as "solitary" or "occurring singly", since this spacing pattern hints of social interactions and territoriality (e.g., Ashmole 1970; Goss-Custard 1985). I judged a species to be *occasionally* territorial if one source indicated that territoriality had been observed. Finally, I categorized a species as *commonly* territorial if multiple sources reported the behaviour from different locations within a species' non-breeding range.

RESULTS

Taxonomic distribution

Territoriality has been reported for 52 (24%) species comprising 21 higher taxa of shorebirds (Figure 1). Most (81%) of these accounts are from the primary literature (Table 1), although evidence for territoriality in 10 species (*Haematopus chathamensis*, *Himantopus novaezelandiae*, *Charadrius hiaticula*, *C. bicinctus*, *C. leschenaultii*, *C. obscurus*, *Vanellus indicus*, *V. spinosus*, *Calidris subminuta*, *Chionis minor*) exists in Cramp *et al.* (1983) and del Hoya (1996). The largest proportions of territorial species occur in the families Charadriidae (29%) and Scolopacidae (27%). Among lapwings and plovers, the proportion of territorial species is slightly higher in the Charadriinae (34%) than the Vanellinae (24%). Within the sandpipers, territoriality is most prevalent in the tringine (65%) and calidridine (50%) sandpipers. By contrast, non-breeding territoriality does not occur or has not been reported in 76% (163 species) of shorebirds and 8 of 13 families. Four of these families, however, are represented by one (3) or two (1) species only.

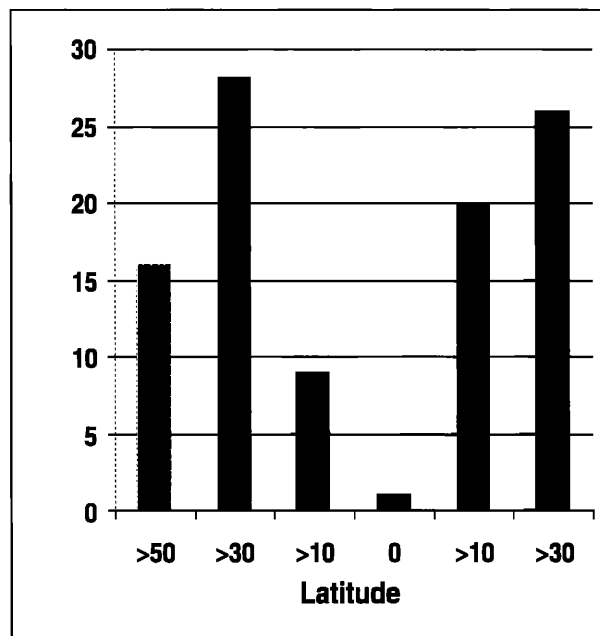


Figure 2. Latitudinal pattern for the occurrence of territoriality in non-breeding shorebirds (see Table 1).



Table 1. Summary of territorial behaviour in nonbreeding shorebirds based on primary literature.

Species		Season ^a	Habitat ^b	Duration ^c	Area ^d	Comments	Source	
<i>Haematopus bachmani</i>	37°44'N 123°02'W	YR	RI	M	NR ^e	Territoriality less during winter	Morrell et al. (1979)	
<i>Charadrius vociferus</i>	Calif.	W	NR	NR	44 m (40-48)		Myers et al. (1979)	
<i>C. melodus</i>	30°15'N 88°11'W	Sep-Apr	IF	NR	NR	Territorial <5% of activity budget, mostly Nov-Feb	Johnson & Baldassarre (1988)	
<i>C. alexandrinus</i>	Calif.	W	NR	NR	108 m (70-145)		Myers et al. (1979)	
<i>C. semipalmatus</i>	N. Amer.	NR	NR	NR	NR		Recher & Recher (1969)	
	Calif.	W	NR	NR	0.01-0.05; 20 m (16-30)		Myers et al. (1979)	
	13°40' S 76°08' W	NR	NR	NR	NR		Myers & McCaffery (1984)	
<i>C. falklandicus</i>	37°23'S 57°12'W	W	OB, IF, TS, FW,	NR	10-70 m	Very commonly territorial	Myers & Myers (1979); Myers et al. (1979)	
<i>C. mongolus</i>	Sov. Union	M	NR	NR	NR		Panov (1963)	
<i>Zonibyx modestus</i>	37°23'S 57°12'W	W	IF, TS, FW, G	NR	10-100 m		Myers et al. (1979)	
<i>Pluvialis squatarola</i>	32°50' N 117°16'W	Oct-Mar	OB	M	~100 m		Michael (1935)	
	Sov. Union 37°23'S 57°12'W	W	NR IF	NR NR	NR NR	Occasionally territorial ¼-½ birds territorial; prey = Nereis, detected visually 65% birds territorial; prey = Upogebia, detected visually	Panov (1963) Myers & Myers (1979)	
	54°38'N 0°11'W	Aug-Apr	IF	D, M; Variable	NR		Townshend (1985); Byrkjedal & Thompson (1998)	
	34° S 26° E	Sep-May			NR		0.05-0.28	Turpie (1995)
	13°40' S 76°08' W	Mar	IF		NR			Myers & McCaffery (1984)
	54°37'N 1°12'W	Jan-Mar	IF		M, D		NR	Wood (1986)
37°23'S 57°12'W	W	OB, IF, TS		NR	125 m (80-300)		Myers et al. (1979)	
<i>P. fulva</i>	21°N 158°W	Aug-May	G	M	0.05-0.40	~50% pop. territorial; mostly adult ♂♂; adult E & juveniles tended to be non-territorial	Johnson et al. (1981); Johnson et al. (1989)	
<i>P. dominica</i>	37°23'S 57°12'W	W	FW, G	NR	0.1-0.3		Myers & Myers (1979); Myers et al. (1979); Byrkjedal & Thompson (1998)	
<i>Vanellus vanellus</i>	~55° N ~8° E	Sep	IF	D	2-3 m		Lind (1957)	
<i>V. melanopterus</i>	29°30'S 30°30'E	All year (Oct-Jul)	G	M	0.56-0.83	Shared with <i>V. coronatus</i> ; ♂, E; A, J	Ward & Maclean (1988)	
<i>V. coronatus</i>	29°30'S 30°30'E	All year (Oct-Jul)	G	M	0.56-0.83	Shared with <i>V. melanopterus</i> ; ♂, E; A, J	Ward & Maclean (1988)	
<i>V. chilensis</i>	37°23'S 57°12'W	W	IF, TS, FW	NR	NR		Myers & Myers (1979); Myers et al. (1979)	
<i>Numenius phaeopus</i>	8°57'N 79°34'W	Jan-Mar	IF	M	0.15-1.07	95% defense against conspecifics; main prey = crabs	Mallory (1982)	
	10°40'N 63°46'W	Jul-Feb	IF	D, M	NR	Nocturnal feeding on Fiddler Crabs	McNeil & Rompré (1995)	
	13°40' S	Mar	IF	NR	NR		Myers &	



N madagascariensis	76°08' W						McCaffery (1984)
	38°S 145°E	W	IF	NR	NR	E	Dann (1987)
N. arquata	53°25'N 6°04'E		IF	D, M	0.3-1.0	Territories abandoned for flock feeding; main prey = Nereis	Ens & Zwarts (1980)
	50°N 3°E	Jul-Apr	IF	M	NR	Up to 20% pop. territorial	Ens (1983)
	54°37'N 1°12'W	Aug-Apr	IF	D, M	NR	Larger EEmore likely to hold territories & feed on polychaetes	Townshend (1981)
N americanus	40°44'N 124°10'W	Jun-Apr	IF	M	0.2 - 4.7	Most territories abandoned in winter; prey = crabs, shrimp, marine worms, fish, bivalves	Colwell et al. (in review)
Limosa haemastica	37°23'S 57°12'W	W	FW, G	NR	NR		Myers et al. (1979)
Catoptrophorus semipalmatus	N. Amer.	NR	NR	NR	NR		Recher & Recher (1969)
	10°40'N 63°46'W	Jul-Feb	IF	D, M	NR	Nocturnal feeding on Uca detected visually	McNeil & Rompré (1995)
	Calif.	W	NR	NR	211 m (80-300)		Myers et al. (1979)
Tringa cinereus	Sov. Union	M	NR	NR	NR		Panov (1963)
T stagnatilis	16°S 16°E	Jan-Feb	FW	NR	0.15	Prey = chironomids	Hötker (1990)
T glareola	55°N 19°E	Late Oct	SE	D	Few m ²		Chojnacki & Kalejta-Summers (1999)
T ochropus	31°17' N 7°58' W	Nov	FW	NR	NR	Most non-territorial	Ormerod & Tyler (1988)
T totanus	~55°N 2°W	Aug-Apr	RI	NR	1.2		Goss-Custard (1970, 1976)
	~55°N 2°W	Aug-Apr	RI	NR	1.2	Territories abandoned when predator present	Whitfield (1988)
T flavipes	37°23'S 57°12'W	W	FW, TS	NR	0.1-0.5; 100 m	"Many defended feeding territories"	Myers & Myers (1979)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
T melanoleuca	13°40' S 76°08' W	Mar	IF	NR	NR	"Many defended feeding territories"	Myers & McCaffery (1984)
	37°23'S 57°12'W	W	IF, FW	NR	NR		Myers & Myers (1979)
	37°23'S 57°12'W	W	TS, FW	NR	NR		Myers et al. (1979)
Actitis hypoleucos	Africa	Winter; Autumn	RS	NR	30-80 m	Possible long-term defense	Simmons (1951)
	Sov. Union	M	NR	NR	NR		Panov (1963)
A macularia	Panama	W	NR	NR	NR		Wetmore (1965)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
Heteroscelus incanus	Sov. Union	M	NR	NR	NR		Panov (1963)
	Calif.	Winter	RS	NR	NR		Myers et al. (1979)
Calidris pusilla	18°57'N 67°12'W	Sep-Nov	SF	NR	3.3-4.8 m	5-14% birds territorial; prey = Trichocorixa & Artemia	Tripp & Collazo (1997)
	N. Amer.	NR	NR	NR	NR		Recher & Recher (1969)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
C mauri	37°26'N 122°08'W	NR	NR	NR	NR	3♂, 2E observed	Recher & Recher (1969)
	18°57'N	Sep-Nov	SF			2-4% territorial	Tripp & Collazo



	67°12'W						(1997)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
<i>C. minuta</i>	36°N 14°E	Apr-May	FW	D	20x20 m	Several adults	Sutherland & Brooks (1981)
	54°N 1°	Sep	FW	D	10x20 m	Single juvenile	Catley (1981)
<i>C. minutilla</i>	18°57'N 67°12'W	Sep-Nov	SF	NR	NR	12-15% birds territorial	Tripp & Collazo (1997)
<i>C. melanotos</i>	50°14' N 98°7' W	Jul-Aug	FW	D	0.001-0.04	Territory locations shifted <10 cm d ⁻¹	Hamilton (1959)
	37°23'S 57°12'W	Winter	FW	NR	0.01-0.05	Most territorial; abandoned as pond dried	Myers & Myers (1979)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
	37°23'S 57°12'W	W	FW	NR	NR		Myers et al. (1979)
<i>C. bairdii</i>	37°23'S 57°12'W	W	FW, SP	NR	0.03 ha	One territorial bird observed	Myers & Myers (1979)
<i>C. ruficollis</i>	Sov. Union	M	NR	NR	NR		Panov (1963)
<i>C. fuscicollis</i>	37°23'S 57°12'W	W	IF, TS, FW	M	0.01-0.05	46% birds territorial; many territorial birds; 14 birds defended an average of 14 d	Myers & Myers (1979); Myers et al. (1979)
<i>C. alba</i>	N. Amer.	Spring	IF	H	Small, linear	Territories based on <i>Limulus</i> eggs	Recher & Recher (1969)
	37°23'S 57°12'W	W	OB	NR	NR	A few territorial birds	Myers & Myers (1979); Myers et al. (1979)
	Calif.	W	OB	M	41 m (12-89)		Myers et al. (1979)
	Calif.	W	IF	M	27 m (18-31)		Myers et al. (1979)
	Calif.	W	OB	1-2 h	5 m (2-10)		Myers et al. (1979)
	38°19'N 123°04'W		OB	D	0.01-0.1	Mode=10 d; some for several weeks	Myers et al. (1979)
	13°40' S 76°08' W	Mar	IF	NR	NR		Myers & McCaffery (1984)
<i>Limicola falcinellus</i>	~20°S ~15°E		Beach				Becker et al. (1974)
<i>Tryngites subruficollis</i>	37°23'S 57°12'W	Aug-Dec	G	D, M	0.01-0.3	Γ, E; clumped dispersion	Myers & Myers (1979); Myers et al. (1979); Myers (1980)

^a Season: YR = year round; W = winter; F = fall, S = spring; M = migration, otherwise months of study presented.

^b Habitat: RI = rocky intertidal, OB = ocean beaches, G = grasslands, pastures, mowed lawns, uplands, runways, SF = salt flats, IF = intertidal flats, including mangroves and other lagoons with of varying substrates, RS = river shoreline; C = channel, SE = sewage pond; FW = freshwater wetland; TS = tidal slough.

^c Duration: H = hours; D = days; M = months; Y = year-round; V = individuals vary (H, D, M).

^d Area of territory in hectares, otherwise reported as linear meters; range of values in parentheses.

^e Not reported.



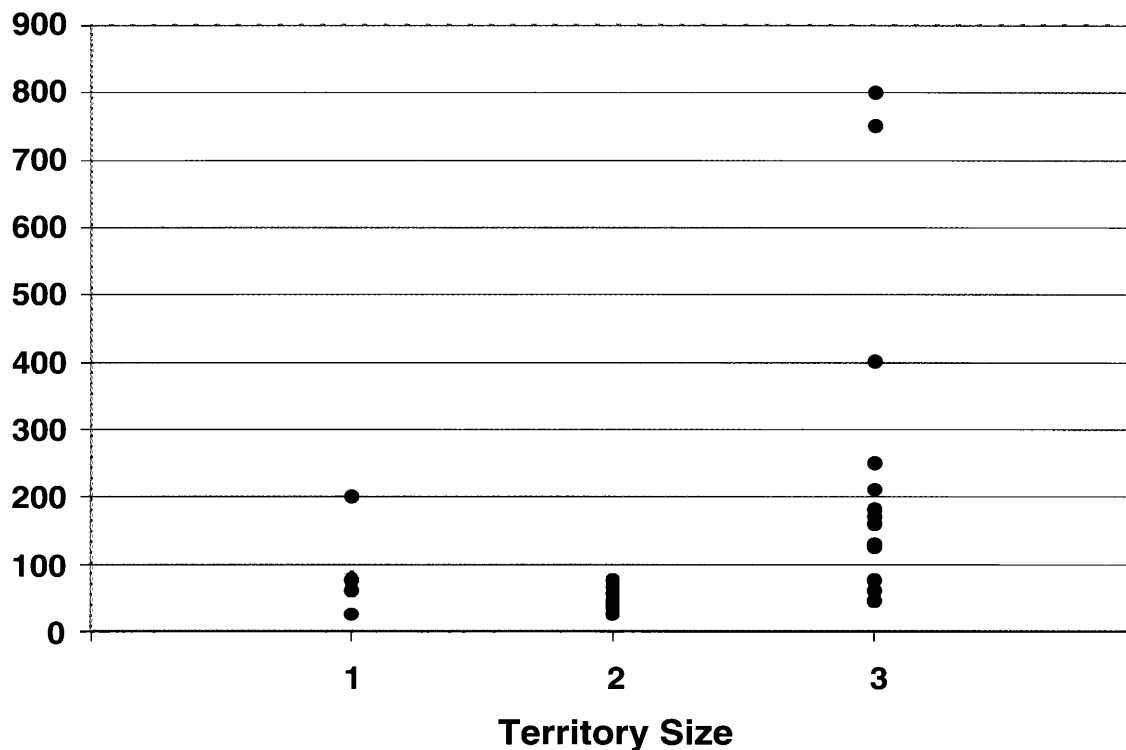


Figure 3. Relationship between body size (mid-range of mass for males and females) and territory size (1 = <0.01 ha; 2 = <0.1 ha; 3 = <1 ha) for 27 species (see Table 1).

Territoriality occurred across a latitudinal range spanning 57° north to 37° south. A disproportionate percentage (69%) of the 68 separate accounts of territoriality comes from latitudes exceeding 30° in both hemispheres (Figure 2; $X^2 = 20.4$, $df = 5$, $P = 0.001$). The greatest proportion of territorial observations was of winter residents (76%), with far fewer observations during fall (13%) and spring (5%) migration. Duration of territory defence varied greatly. Long-term defence of territories occurred in some species (e.g., *Haematopus bachmani*, *H. chathamensis*, *Himantopus novaezelandiae*) where individuals occupied year-round territories, which functioned for feeding and breeding. In other species (e.g., *Pluvialis squatarola*, *P. fulva*, *Numenius arquata*), individuals returned year after year to defend winter feeding territories for months. By contrast, individuals of some species (e.g., *Calidris pusilla*, *C. mauri*, *C. minutilla*) defended territories for hours. Overall, however, it was difficult to compare duration of defence because of the short-term nature of most studies. Territory size varied from small (<5 m) linear stretches of shoreline to large areas (~1 ha) of intertidal flats. There was a tendency for larger species to defend larger areas (Figure 3). Most species defending territories detected prey visually (e.g., plovers, lapwings, tringines and calidridines); very few species (e.g., *Limosa haemastica*) that typically detect prey using tactile cues defended territories.

DISCUSSION

Two decades ago, Myers and his colleagues stated that “many shorebirds defend territories in winter” and that “non-breeding territoriality is widespread in shorebirds” (Myers *et al.* 1979; Myers 1984). Since these reviews, approximately 15 additional papers have been published providing details on non-breeding territoriality. Many of these recent accounts, however, merely document additional instances in species already known to be territorial. For example, Myers (1984) addressed variation in territorial behaviour associated with habitat and individual attributes (e.g., size) of black-bellied plovers wintering in northeast England (Townshend 1985). Recent publications on wintering black-bellied plovers at both the northern (Wood 1986) and southern extreme of their wintering range (Turpie & Hockey 1993; Turpie 1995) confirm the widespread occurrence of territoriality in this species. Similarly, additional evidence of territoriality has been reported for one plover (Johnson *et al.* 1981, 1989), several calidridine sandpipers (Tripp & Collazo 1997), two tringine sandpipers (Whitfield 1988; McNeil and Rompré 1995) and two curlews (Townshend 1981; McNeil & Rompré 1995).

New (since Myers *et al.* 1979) evidence of territoriality comes from three plovers (Johnson & Baldassarre 1988; Ward and Maclean 1988), two curlews (Dann 1987; Colwell *et al.* in review), two tringine sandpipers (Hötker 1990; Chojnacki & Kalejta-Summers 1999) and one calidridine sandpiper (Sutherland & Brooks 1981; Catley



1981). These new accounts strengthen the observation of Myers *et al.* (1979) that territoriality is more common in some groups than others (Figure 1). Territoriality is most prevalent in plovers, tringine sandpipers, calidridine sandpipers, and curlews; it is absent from eight families and four tribes of the Scolopacidae. Hence, a clear taxonomic pattern exists, which suggests that additional accounts will likely come from groups already recognized as exhibiting territoriality.

Territoriality and feeding method

One noteworthy correlate of territoriality is that it is prevalent in species that use visual cues to detect prey (Recher & Recher 1969; Stinson 1980; Goss-Custard 1985). Intraspecific variation in territorial behaviour corroborates the pattern. For example, McNeil & Rompré (1995) showed that territorial willets and whimbrels used visual cues to detect their principal prey (crabs and fishes) in mangrove swamps, especially on moonlit nights when fish were more abundant and visible (compared to dark nights). By contrast, non-territorial willets fed by touch in the same habitats.

Several authors (e.g., Recher & Recher 1969; Stinson 1980; Goss-Custard 1985) have addressed the association between territoriality and visual feeding. Recher & Recher (1969) suggested that visual feeders were more likely to be territorial because they were more able to detect variation in prey abundance (and hence gained knowledge of the value of the resource to be defended) over a larger area compared with species that fed by touch (whose knowledge of prey variation was limited to the immediate foraging location). Furthermore, Goss-Custard (1985) argued that since visual feeders detected prey over large areas, they were more likely to interfere with foraging conspecifics (Goss-Custard 1985). As a result, foraging rates of visual feeders suffered from the presence of conspecifics, which increased the likelihood of aggression and territoriality. Finally, Blick (1980) proposed that territoriality was more likely among visual feeders because they could feed and scan for predators simultaneously. Specifically, deep-probing, tactile feeders can not forage and remain vigilant simultaneously; hence they benefit from flocking. Conversely, visual feeders are more likely to disperse widely and defend food resources. The ability of these explanations to account for territoriality in the wide array of species exhibiting the behaviour undoubtedly varies greatly with food distribution and predation risk (Myers 1984).

Territory size and duration of defence

Considerable interspecific variation in territory size correlated with species' size (Figure 3). Large species (e.g., *Numenius spp.*, *Pluvialis spp.*) tended to defend larger areas for longer periods compared to small species (e.g., *Calidris spp.*, *Tringa spp.*). Moreover, territoriality

in most large species occurred at wintering sites, whereas instances in several small sandpipers came from migration stopover sites. These differences probably relate to the size, spatial distribution and predictability of prey of different species of shorebird. For example, large curlews and plovers defended food resources consisting of large prey (e.g., crabs, shrimp, and polychaetes) often resident in permanent burrow systems. Hence, the predictability of the food supply probably influences the expression and duration of territoriality. By contrast, small tringine and calidridine sandpipers defended small, temporary territories around relatively small prey (e.g., chironomids, *Artemia*, and *Trichocorixa*) in ephemeral habitats. The common occurrence of territoriality in large species and opportunistic occurrence in small taxa indicate that the characteristics of prey are important influences on interspecific variation.

CONCLUSION

Territoriality represents one extreme of wader dispersion patterns in which hyper-dispersed individuals vigorously defend food resources; toward the other extreme are aggregations of birds in flocks of increasing density (Myers 1984; Goss-Custard 1985). The ultimate factors shaping these dispersion patterns are predation risk and patchy food distribution (Myers 1984; Goss-Custard 1985). Among territorial species, the expression of territoriality (i.e., frequency, size of territory, duration of defence) appears to be influenced by species' characteristics (e.g., body size and diet), as well as habitat features (e.g., predation risk, food distribution and habitat). Territoriality has been observed in only 24% of wader species, and it is clearly more common in some taxa than others. Territoriality is a regular feature of the non-breeding biology of a limited number of species throughout their winter range. I predict additional instances of territoriality will come from these groups.

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