Aggressive behaviour of migrant and resident waders at the Berg River estuary, South Africa

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Aggressive interactions among and between migrant and resident waders were described at a south temperate estuary in South Africa. Intraspecific interactions accounted for 91% of all aggressive encounters observed. Overall, chase was the most common form of aggression for conspecifics except for Curlew Sandpiper, which displaced more than chased. In the austral summer, aggression was more intense amongst visual than tactile foragers: chases and attacks predominated in their encounters. Ninety-one percent of all interspecific interactions were initiated by visual foragers. Chases and displacements were the most common form of aggression between species during summer and chases predominated in winter. The significance of aggression in influencing distribution of birds with different foraging techniques is discussed.

INTRODUCTION

Aggressive interactions are important in influencing the spacing behaviour of waders (Goss-Custard 1970, Burger *et al.* 1979). It has been implied that visual-feeding birds are well dispersed on their foraging grounds because they are more susceptible to intraspecific aggression than tactile-feeding birds, which typically forage in dense flocks (Recher & Recher 1969, Goss-Custard 1970). In a more recent study, Young (1989) suggested that aggression intensity rather than frequency plays a major role in determining spacing behaviour in waders.

Most studies of aggression between waders have concentrated on migratory species during the nonbreeding season when they form large, mixed-species assemblages (Burger, *et al.* 1979, Stawarczyk 1984, Metcalfe & Furness 1987). At this time of the year, migrant waders are often sympatric with resident congeners.

This study describes the aggressive interactions of migrant and resident waders on a seasonal basis at a south temperate estuary. Intensity of aggression is examined in relation to birds with different foraging techniques.

STUDY SITE AND METHODS

The study was carried out at the Berg River estuary, Western Cape, South Africa (32°7'S, 18°0'E), close to the southern limit of the Palearctic–Afrotropical migration routes. Here, migrant waders forage on the intertidal mudflats alongside resident species, which occupy the estuary throughout the year (Velasquez *et al.* 1991, Appendix 1). The migrant birds begin to arrive on the estuary at the beginning of October and stay until April the following year. A proportion of immature birds does not return to their breeding grounds in their first year and remains on the estuary during the austral winter (Appendix 1).

The study was conducted from May 1988 to April 1989, and covered one austral winter (May–August) and one summer (September–April). Four intertidal study sites (25 × 80 m) were demarcated at increasing distances from the river mouth and at distances between 300 m to 1 km of each other. Twice a month, birds were observed in each study site through a 22× telescope from a distance of 10–30 m during low tide, which lasted from 4 to 8 hours. The study sites were scanned at 20-minute intervals and the number of foraging birds was recorded. Between the scans, observations on feeding activities of birds were conducted during one-minute focal animal observations. Data on the foraging activities of birds have been published elsewhere (Kalejta 1992a, Kalejta 1993a, Kalejta & Hockey 1994). Between the observations on foraging, aggressive interactions amongst birds were recorded using a tape-recorder. The following parameters of aggression for each interaction were described:

I Which species was the aggressor and which the recipient.

II The type of encounter scored on a 5-point scale of increasing intensity:

(1) Threat: a threat posture only.
(2) Displacement: one bird forces another bird to move from its foraging site.
(3) Chase: one bird chasing another.
(4) Attack: one bird physically attacking another, either on the ground or from the air.
(5) Fight: the recipient of an attack retaliating.

The birds were classed as visual or tactile foragers (Appen-

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Table 1. Intraspecific aggressive encounters (threats, displacements, chases, attacks and fights) amongst migrant and resident waders at Berg River estuary during winter (May–August 1988) and summer (September 1988–April 1989). The species are arranged in order of decreasing body mass.

	Winter					
	Percentage (%)					Total number of interactions
	Threat	Displacement	Chase	Attack	Fight	
Greenshank	0.0	40.0	40.0	10.0	10.0	10
Black-winged Stilt	0.0	0.0	46.7	33.3	20.0	15
Blacksmith Plover	25.8	6.5	41.9	22.6	3.2	31
Curlew Sandpiper	0.0	44.4	22.2	33.3	0.0	9
White-fronted Plover	0.0	18.2	78.8	3.0	0.0	33
Kittlitz's Plover	0.0	6.1	59.8	31.2	2.9	311
Chestnut-banded Plover	0.0	0.0	0.0	100.0	0.0	2
	Summer					
Grey Plover	8.3	8.3	58.3	25.0	0.0	12
Greenshank	0.0	26.7	46.7	20.0	6.7	15
Ruddy Turnstone	0.0	0.0	100.0	0.0	0.0	1
Curlew Sandpiper	3.8	55.7	31.6	1.3	7.6	79
Ringed Plover	7.7	7.7	46.2	15.4	23.1	13
White-fronted Plover	0.0	6.5	71.0	19.4	3.2	31
Kittlitz's Plover	0.0	0.0	75.0	25.0	0.0	4
Little Stint	0.0	100.0	0.0	0.0	0.0	1

dix 1). Greenshank, Marsh Sandpiper and Black-winged Stilt were seen using both visual and tactile foraging techniques. However, since tactile feeding predominated in their foraging, they were classified as tactile foragers. (For scientific names of species mentioned in this paper, refer to Appendix 1).

Because the rate of aggressive encounters could not be calculated, all the analyses were performed on the percentages of the different types of aggression. A multivariate regression analysis was carried out to find out whether variation between conspecifics in the percentage of high-intensity aggression (chases, attacks and fights combined) was related to feeding technique (visual vs. tactile foragers), migration status (migrant vs. resident birds) or body size. The analysis was performed separately for summer and winter because the suite of species was largely different in each season. A step-up procedure was used to determine the most appropriate model.

RESULTS

Intraspecific aggression

Ninety-five percent and 81% of all aggressive interactions were between conspecifics in winter and summer, respectively (Tables 1 and 3). All the encounters involved feeding space and the initiator was always the winner. Kleptoparasitism was not observed.

Eleven species of waders were involved in intraspecific encounters. Apart from the Curlew Sandpiper, chase was the most common form of aggression for all species (29% and 51% of all intraspecific encounters in summer and winter, respectively) (Table 1). Threat postures were the rarest and accounted for 3% and 2% of all intraspecific encounters in summer and winter, respectively. Curlew Sandpiper was the only species that displaced more than chased in both summer and winter (56% and 44% of all the intraspecific encounters, respectively) (Table 1).

In summer, when the overall density of waders was at its highest, feeding technique was the only significant explanatory variable for the observed variation in intensity of aggression; visual foragers were involved in proportionally more intensive aggressive encounters (chases, attacks and fights combined) than tactile foragers (Table 2; $F_{1,6}$=11.2, p=0.015). Even, with the exclusion of the Little Stint and Turnstone where the sample sizes were only 1, the relationship was significant ($F_{1,4}$ = 8.2, p=0.046). In winter, none of the variables explained the variation in the intensity of aggression.

In summer, the percentage of attacks and fights (the most intense forms of aggression) was highest in Ringed Plovers (39% of all the encounters). The lowest contribution of attacks and fights to the overall aggression was shown by Curlew Sandpipers (9%). In winter, Black-winged Stilts had a highest percentage of attacks and fights in their overall aggression (53% of all the encounters). The intensity of aggression was lowest for White-fronted Plovers. They did not fight at all, and attacks formed only 3% of all their aggressive encounters.

There was a significant positive relationship between the number of aggressive intraspecific interactions observed and the density of birds in winter (Table 1, Appendix 1) (r_s = 0.857, n = 7, p<0.05) but not in summer (r_s = 0.671, n = 8, ns).

Interspecific aggression

Eight species were involved in interspecific aggressive interactions. In summer, combined displacements and chases contributed most to all the encounters (81%) and chases predominated in winter (65% of all the aggressive encounters). Fights were not observed (Table 3). In 91% of all the interspecific encounters visual foragers were the initiators.

Size-related dominance in aggression was well pronounced: in 39 out of 56 interspecific encounters (70%), the larger species was the aggressor (χ^2 = 7.9, df = 1, p<0.01) (Tables 3 and 4). Of those, Grey Plovers were involved in 24

Table 2. High-intensity aggressive intraspecific encounters during the austral summer as a percentage of all intraspecific encounters compared with feeding technique, status and body mass.

	% of high-intensity aggressive encounters (N)	Technique	Status	Mass
Grey Plover	83.3 (12)	Visual	Migrant	216
Greenshank	73.4 (15)	Tactile	Migrant	191
Turnstone	100 (1)	Visual	Migrant	99
Curlew Sandpiper	40.5 (79)	Tactile	Migrant	57
Ringed Plover	84.7 (13)	Visual	Migrant	55
White-fronted Plover	93.6 (31)	Visual	Resident	49
Kittlitz's Plover	100 (4)	Visual	Resident	43
Little Stint	0 (1)	Tactile	Migrant	24

(43%) of all the encounters. There was, however, no relationship between the intensity of aggression and the body size of the aggressor (Table 3, Appendix 1). Of all the interspecific aggression initiated by migrant waders, 35% was directed at residents (Table 4). Of those, 70% took place in summer. By contrast, 52% of all interspecific aggression initiated by resident waders was directed at migrants and 79% of those occurred in summer. In summer, 47% of all the interactions were between migrant species. Of all the aggressive interactions in winter, 60% were between resident species.

DISCUSSION

Morphologically similar individuals are likely to utilise similar food resources or foraging microhabitats, and are thus more likely to be involved in aggressive encounters over these resources than are morphologically dissimilar individuals (Recher & Recher 1969). This concords with the observation in this study in that most aggressive interactions were between individuals of the same species. Furthermore, fights, the most intensive type of aggression, were quite common between conspecifics but did not occur between the interspecifics (Tables 1 and 3). This implies that competition might be greater amongst individuals of the same species than individuals of different species. As in this study, others have shown that larger species are more likely to initiate and win aggressive interactions (Burger *et al.* 1979, Stawarczyk 1984, Metcalfe & Furness 1987).

Visual foragers vs. tactile foragers

Foraging techniques of birds are an important factor influencing the intensity of aggression. Because visual foragers can detect prey from a greater distance than tactile foragers, they should maintain a greater individual distance from conspecifics and be more aggressive in defence of this personal space (Recher & Recher 1969, Goss-Custard 1970). As a result, visual-feeding birds tend to forage solitarily or in small loose flocks (Stinson 1980). At the Berg River estuary, visual foragers were involved in more intensive intraspecific aggressive interactions than tactile foragers. Similar differences in the intensities of aggression between tactile and visual foragers were recorded by Young (1989). Stinson (1977) and Vines (1980), on the other hand, have shown that visual-feeding Grey Plovers use avoidance behaviour to

Table 3. Interspecific aggressive encounters (threats, displacements, chases, attacks and fights) perpetrated by migrant and resident waders at Berg River estuary during winter (May–August 1988) and summer (September 1988–April 1989). The species initiating each encounter are arranged in order of decreasing body mass.

	Winter					
	Percentage (%)					Total number of interactions
	Threat	Displacement	Chase	Attack	Fight	
Grey Plover	0.0	0.0	100.0	0.0	0.0	1
Black-winged Stilt	0.0	0.0	0.0	100.0	0.0	1
Blacksmith Plover	0.0	0.0	70.0	30.0	0.0	10
Curlew Sandpiper	0.0	50.0	50.0	0.0	0.0	2
White-fronted Plover	0.0	0.0	100.0	0.0	0.0	3
Kittlitz's Plover	0.0	33.3	33.3	33.3	0.0	3
	Summer					
Grey Plover	4.5	13.6	63.6	18.2	0.0	22
Greenshank	0.0	100.0	0.0	0.0	0.0	1
Blacksmith Plover	0.0	0.0	0.0	100.0	0.0	1
Curlew Sandpiper	0.0	100.0	0.0	0.0	0.0	1
Ringed Plover	0.0	50.0	0.0	50.0	0.0	2
White-fronted Plover	0.0	28.6	71.4	0.0	0.0	7
Kittlitz's Plover	0.0	100.0	0.0	0.0	0.0	2

Table 4. The number of interspecific interactions between waders observed at the Berg River estuary from May 1988 to April 1989. The initiator always won the encounter.

Aggressor	Recipient	Number of interactions	
		winter	summer
Migrant wader	**Migrant wader**		
Grey Plover*	Greenshank	2	1
Grey Plover*	Curlew Sandpiper	0	4
Grey Plover*	Ruddy Turnstone	0	6
Grey Plover*	Ringed Plover	0	3
Curlew Sandpiper*	Little Stint	0	1
Greenshank*	Curlew Sandpiper	0	1
Ringed Plover	Curlew Sandpiper	0	1
Migrant wader	**Resident wader**		
Grey Plover*	Blacksmith Plover	0	3
Grey Plover*	Kittlitz's Plover	1	1
Grey Plover*	White-fronted Plover	0	2
Curlew Sandpiper*	Kittlitz's Plover	1	0
Curlew Sandpiper*	White-fronted Plover	1	0
Ringed Plover*	White-fronted Plover	0	1
Resident wader	**Resident wader**		
Blacksmith Plover	Black-winged Stilt	1	1
Blacksmith Plover*	Kittlitz's Plover	8	0
White-fronted Plover*	Kittlitz's Plover	3	0
Resident wader	**Migrant wader**		
Black-winged Stilt	Greenshank	0	1
Blacksmith Plover	Grey Plover	0	1
Kittlitz's Plover	Curlew Sandpiper	3	2
White-fronted Plover	Curlew Sandpiper	0	5
White-fronted Plover	Ringed Plover	0	1
White-fronted Plover	Marsh Sandpiper	0	1

* encounters initiated by the larger species.

maintain intraspecific spacing and, consequently, most aggression is directed interspecifically. At the Berg River estuary, 91% of interspecific interactions were initiated by visual foragers (Table 3).

Of all the visual foragers present at the Berg River estuary, only migrant Grey Plover showed a strong tendency to form territories (per. obs.). Recher & Recher (1969) showed that territorial birds are more aggressive in defending their personal space than non-territorial individuals. In this study, the non-territorial Ringed Plover had the largest proportion of high intensity aggression (Table 1). However, since the rate of aggression is unknown, it is not possible to conclude that this was the most aggressive species.

In contrast to visual foragers, tactile foragers usually form large and dense flocks (Myers 1984, Goss-Custard 1976). Stinson (1980) suggested that the threat of predation is a major selective pressure influencing flocking behaviour in foraging waders, whereas Whitefield (1988) argues that benefits of flocking extend beyond merely increasing the probability of predation detection. At the Berg River estuary, African Marsh Harriers *(Circus ranivorus),* and Peregrine and Lanner Falcons *(Falco peregrinus* and *F. biarmicus)* regularly hunt over the intertidal mudflats and were seen, on several occasions, attacking flocks of feeding birds (pers. obs.). Curlew Sandpipers, tactile foragers and the most abundant species on the Berg River estuary, concentrate at the site with the highest abundance of their preferred prey *Ceratonereis keiskama* (Kalejta & Hockey 1994). Their aggression was of low intensity in comparison with other species and displacements contributed most to their aggression (Table 1). It is likely that, at high prey densities, Curlew Sandpipers may tolerate the close proximity of conspecifics if any advantage they gain from flocking in terms of predation detection outweighs any advantage they could gain from aggressive displacement of neighbours.

Migrant waders vs. resident waders

Although coexistence between resident and migrant species has been studied with regard to diet (Kalejta 1993b) and foraging microhabitat (Strauch & Abele 1979), the influence of aggression on their coexistence or segregation is poorly understood. Seventy percent of interspecific aggression initiated by migrant waders in this study was directed at residents during summer. Similarly, 79% of all the aggressive encounters initiated by residents were directed at migrants, also during summer. This is the time of year when migrant waders are in their highest densities and residents are at their lowest (Appendix 1). This is also time of the year when abundance and availability of prey is the highest (Kalejta 1992a & b). Since the highest predation pressure by waders at the Berg River estuary during austral summer coincides with the period of the highest production of the most important invertebrate prey (Kalejta 1992a & b, Kalejta 1993b), it is unlikely that observed aggression behaviour is a result of poor food resources. Prey characteristics other than abundance are known to influence aggression. These include prey type, size and distribution (Recher & Recher 1969, Myers

1984). Those parameters differ greatly between the mudflats of the Berg River estuary (Kalejta 1992b, Kalejta & Hockey 1991), but it is unknown how they influence aggression or to what extent aggression varies between those mudflats.

Because of the method by which aggression has been measured in this study, the results must be interpreted with caution. First, it is likely that some aggressive encounters were missed because the observation time was not wholly devoted to recording aggression (see Methods). For this reason, the frequency of aggressive encounters could not be calculated. Second, the frequency of the lowest ranked type of aggression, threat postures, might have been underestimated (not only in this study, but also elsewhere) because they are not as obvious as more intensive forms of aggression, such as attacks or fights. Some of the threat signals involve slight alteration of the head, tail or back feathers and perceiving those depends greatly on the skill of the observer. Third, because aggression is partly influenced by the density of birds and observations were made within small areas, the extent of overall aggression might have been underestimated, especially, in the case of visual foragers who maintain large individual distances.

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REFERENCES

Burger, J., Hawn, D.C. & Chase, J. 1979. Aggressive interactions in mixed-species flocks of migrating shorebirds. *Anim. Behav.* 27: 459–469.

Goss-Custard, J.D. 1970. Feeding dispersion in some overwintering wading birds. In: *Social behaviour in birds and mammals* (Ed: J.H. Crook), pp. 3–35. Academic Press, London.

Goss-Custard, J.D. 1976. Variation in the dispersion of Redshank *Tringa totanus* on their winter feeding grounds. *Ibis* 118: 257–263.

Kalejta, B. 1992a. Time budgets and predatory impact of waders at the Berg River estuary, South Africa. *Ardea* 80: 327–342.

Kalejta, B. 1992b. Distribution, biomass and production of *Ceratonereis erythraeensis* (Fauvel) and *Ceratonereis keiskama* (Day) at the Berg River estuary, South Africa. *S. Af. J. Zool.* 27: 121–129

Kalejta, B. 1993a. Diets of shorebirds at the Berg River estuary, South Africa: Spatial and temporal variation. *Ostrich* 64: 123–133.

Kalejta, B. 1993b. Intense predation cannot always be detected experimentally: a case study of shorebirds predation on nereid polychaetes in South Africa. *Neth. J. Sea Res.* 31: 385–393.

Kalejta, B. & Hockey, P.A.R. 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. *Estuar., Coast. & Shelf Sci.* 33: 175–191.

Kalejta, B. & Hockey, P.A.R. 1994. Distribution of shorebirds at the Berg River estuary, South Africa, in relation to foraging mode, food supply and environmental features. *Ibis* 136: 233–239.

Maclean, G.L. 1985. *Roberts' Birds of southern Africa.* Cape Town: John Voelcker Bird Book Fund.

Metcalfe, N.B. & Furness, R.W. 1987. Aggression in shorebirds in relation to flock density and composition. *Ibis* 129: 553–563.

Myers, J.P. 1984. Spacing behaviour in non-breeding shorebirds. *Shorebirds: migration and foraging behaviour* (Eds: Burger, J. & Olla, B.L.), pp. 271–321. Plenum Press, New York.

Recher, H.F. & Recher, J.A. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. *Wilson Bull.* 81: 140–154.

Stinson, C.H. 1977. The spatial distribution of wintering black-bellied plovers. *Wilson Bull.* 89: 470–472.

Stinson, C.H. 1980. Flocking and predator avoidance: model of flocking and observations on the spatial dispersion of foraging winter shorebirds (Charadrii). *Oikos* 34: 35–43.

Stawarczyk, T. 1984. Aggression and its suppression in mixed-species wader flocks. *Ornis Scand.* 15: 23–37.

Strauch, J.G. & Abele, L.G. 1979. Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. *St. Avian Biol.* 2: 217–230.

Velasquez, C.R., Kalejta, B. & Hockey, P.A.R. 1991. Seasonal abundance, habitat selection and energy consumption of waterbirds at the Berg River estuary, South Africa. *Ostrich* 62: 109–123.

Vines, G. 1980. Spatial consequences of aggressive behaviour in flocks of Oystercatchers, *Haematopus ostralegus L. Anim. Behav.* 28: 1175–1183.

Whitefield, D.P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus. Ibis* 130: 284–287.

Young, A.D. 1989. Spacing behaviour of visual- and tactile-feeding shorebirds in mixed-species groups. *Can. J. Zool.* 67: 2026–2028.

Appendix 1. Average density (birds ha^{-1}) and mass (g) of migrant and resident waders involved in aggressive encounters at the Berg River estuary between May 1988 and April 1989. The densities of waders were extracted from Velasquez *et al.* 1991 and mass was taken from Maclean 1985. Feeding techniques of birds are indicated in brackets; V – visual foragers, T – tactile foragers. Winter extends from May to August and summer from September to April.

	Average density (birds ha^{-1})		Mass (g)
	Winter 1988	Summer 1988/89	
Migrant waders			
Curlew Sandpiper *Calidris ferruginea* (T)	0.56	51.00	57
Little Stint *Calidris minuta* (T)	0.00	3.15	24
Ringed Plover *Charadrius hiaticula* (V)	0.00	4.01	55
Grey Plover *Pluvialis squatarola* (V)	0.22	2.99	216
Greenshank *Tringa nebularia* (T)	1.49	1.76	191
Marsh Sandpiper *Tringa stagnatilis* (T)	0.01	0.42	75
Ruddy Turnstone *Arenaria interpres* (V)	0.00	0.21	99
Resident waders			
Kittlitz's Plover *Charadrius pecuarius* (V)	9.02	1.75	43
White-fronted Plover *Charadrius marginatus* (V)	2.13	3.69	49
Black-winged Stilt *Himantopus himantopus* (T)	1.19	0.28	178
Blacksmith Plover *Vanellus armatus* (V)	0.86	0.03	157
Chestnut-banded Plover *Charadrius pallidus* (V)	0.27	0.00	35