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Aggression in Flocks of Foraging Shorebirds During Spring Stopover at Delaware Bay, USA

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Abstract.—The objective of this study was to examine aggressive behavior of shorebirds during spring stopover on beaches and other stopover habitats in Delaware Bay, New Jersey, USA. More aggressive interactions were observed between members of the same species than between species at all study locations. The incidence of interspecific interactions was higher than previously reported for shorebirds, particularly in Sanderlings (*Calidris alba*), which directed almost half of their attacks toward members of other species, mainly Semipalmated Sandpipers (*Calidris pusilla*). Significantly more heterospecific attacks were directed toward smaller competitors (67%) than toward similarly sized (15%) or larger (18%) competitors. *Received 27 June 2017, accepted 10 October 2017.*

Key words.—horseshoe crab, interference competition, interspecific aggression, migration, shorebirds, species interactions.

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Migrating shorebirds form large, usually mixed-species flocks on feeding grounds along migratory routes (Recher and Recher 1969). Foraging in groups brings several benefits to foragers, mainly in terms of reduced predation risk and foraging benefits, but it also brings costs through increased competition for resources (Beauchamp 2014). The latter may be particularly true for migrating shorebirds while at stopover sites, as they forage on habitats that are often affected by the tidal cycle, forcing birds to feed on restricted areas along intertidal beaches and mudflats simultaneously (Recher and Recher 1969).

In general, competition for resources occurs through depletion and interference (Sutherland 1996). Although early work on competition had put an emphasis on depletion, interference can be equally important in bird communities (Maurer 1984). Usually, interference through aggressive interactions is more common between conspecifics than between heterospecifics, as individuals of the same species compete for mating opportunities and other resources. Likewise, the level of interspecific aggression is more frequent between morphologically similar, congeneric species, and it is positively related to resource overlap (Peiman and Robinson 2010). The outcomes of heterospecific aggressive interactions are often asymmetric and strongly affected by the size of competitors, when larger species, due to interspecific social dominance, gain access to resources by displacing smaller ones (Martin *et al.* 2017). However, smaller species may dominate contests with larger ones when interactions occur between more distantly related species (Martin and Ghalambor 2014).

Heterospecific aggression, although not as prevalent as conspecific aggression, is still common among closely related species, acting as a selective pressure on both species traits and communities (Martin *et al.* 2017). Heterospecific aggressive interactions were rare in mixed-species foraging flocks during fall migration (Recher and Recher 1969; Burger *et al.* 1979) and on wintering grounds (Kalejta-Summers 2002). However, information on interspecific interactions among shorebirds at spring stopovers is relatively scarce.

I studied aggressive interactions in mixed-species flocks of shorebirds at stopovers in Delaware Bay, USA, during spring migration. I tested the predictions that: 1) shorebirds will exhibit more aggression toward conspecific than to heterospecific individuals; and 2) larger species will dominate smaller ones.

Methods

Study Area

The study took place from 12 March to 1 June 2011 and 18 March to 1 June 2012 at four locations in Delaware Bay, New Jersey, USA: Matts Landing (39° 13′

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56.58″ N, 75° 00′ 42.32″ W), Bivalve (39° 14′ 7.63″ N, 75° 02′ 3.88″ W), Thompson's Beach (39° 12′ 10.64″ N, 74° 59′ 36.57″ W) and Fortescue (39° 13′ 21.97″ N, 75° 09′57.88″ W). Matts Landing is an artificial impoundment with an extensive area of soft mud around the water's edge where shorebirds roost during high tides, but also forage, especially in early spring. Thompson's Beach and Bivalve are tidal marshes dominated by grasses (*Spartina* spp.) with exposed mudflats where shorebirds forage during low tides. The habitat in Fortescue is a sandy beach where birds also forage at low tide.

A flock was defined as a group of foraging shorebirds up to 10 m apart from each other. To record aggressive interactions, I scanned foraging flocks with a digital camera (Panasonic HDC-TM60, optical zoom 35X) from an approximate distance of 15-60 m, depending on recording location and the tidal cycle. Foraging flocks were recorded either along transects or from one point at regular intervals, ranging from 10 to 30 min when possible. If individuals were flushed, I waited for them to settle down and continued scanning after they had landed or ceased recording if birds flew away.

Video Analysis

I analyzed videos in 1/4 to 1/8 speed slow motion. All videos were reviewed several times to insure the accuracy of collected data. Duration of videos depended on the number of foraging birds and the area they occupied, ranging from 12 to 215 sec (median 54 sec). From each video, I recorded the number of aggressive interactions and identified the attacker, defender, and winner to species. If the attacker interacted with more than one individual (e.g., a bird displaced two individuals simultaneously), the interaction was recorded as a single act. In spite of interspecific differences in postures and movements of birds engaged in agonistic behavior, I was able to recognize several aggressive acts between foraging individuals and to ascribe them to all shorebird species (Table 1). In most cases, one scan video contained one foraging flock, although foraging birds were occasionally separated in two distinct groups that were treated as different flocks. As the focus of this study was on heterospecific aggression, only flocks of two or more species, where one species did not constitute more than 90% of a flock, were included in analyses.

Data Analysis

To assess differences in the total number of intraspecific and interspecific aggressive interactions, I used zero-inflated negative binomial model as the data set was zero-inflated (Zuur and Ieno 2016). I tested for differences in per-capita rates of aggressive interactions between study species using negative binomial generalized linear model. To account for variability in flock size, I specified an offset variable as the number of foraging birds within the flock (Zuur and Ieno 2016).

To test for difference in the size of competitors, as well as in the outcomes of aggressive contests, I used binomial tests (Crawley 2013). Based on the body size and mass, Red Knots, Ruddy Turnstones and Short-billed Dowitchers (hereafter turnstones, dowitchers and knots, respectively) were considered larger species (Nettleship 2000; Jehl *et al.* 2001; Baker *et al.* 2013), Dunlins and Sanderlings were considered medium-sized (Warnock and Gill 1996; Macwhirter *et al.* 2002), and Semipalmated Sandpipers (hereafter sandpipers) were the smallest of shorebirds observed in foraging flocks (Hicklin and Gratto-Trevor 2010) (scientific names in Table 2).

To determine the effect of the proportion of different shorebird species on the number of heterospecific aggressive interactions within foraging flocks, I used generalized linear mixed model (GLMM) with a negative binomial distribution. Prior to the analysis, I checked for outliers and collinearity between the explanatory variables. The data set was log-transformed prior to analysis. The model included the number of interspecific interactions as the response variable, and the proportion of turnstones, knots, Sanderlings, Dunlins, sandpipers, and dowitchers as explanatory variables. In addition, I included an offset variable specified as the number of foraging birds within the flock, and a random effect specified as a date of recording to account for environmental conditions that may influence aggressive behavior (Bettini and Norris 2012; Peluso *et al.* 2013).

Table 1. Descriptions of foraging and interacting shorebirds (modified from Recher and Recher 1969).

Behavior	Description
Threat display	The focal bird keeps individual distance by movements directed toward the intruder, usually with erected feather and slightly raised wings.
Displacement without poking or hitting	The focal bird rapidly moves toward the rival, displacing it from the feeding area without poking it, hitting it or achieving any other kind of physical contact.
Poking or hitting, with or without displacement	The focal bird rapidly moves toward the rival, displacing it from the feeding area by pushing it using chest or poking it using bill or the focal bird pokes or hits the rival, without displacing it from the feeding area.
Chasing	The focal bird rapidly chases the rival.
Fight	The focal bird actively fights with the rival.

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Table 2. Proportions of aggressive encounters among shorebirds (sample size).

Attacking Species	Attacked Species	% (*n*)
Ruddy Turnstone (*Arenaria interpres*)	Ruddy Turnstone	65.9 (426)
	Red Knot	4.8 (31)
	Sanderling	8.3 (54)
	Dunlin	4.2 (27)
	Semipalmated Sandpiper	16.4 (106)
	Short-billed Dowitcher	0.3 (2)
Red Knot (*Calidris canutus*)	Ruddy Turnstone	10.8 (12)
	Red Knot	60.4 (67)
	Sanderling	9.0 (10)
	Dunlin	3.6 (4)
	Semipalmated Sandpiper	11.7 (13)
	Short-billed Dowitcher	4.5 (5)
Sanderling (*Calidris alba*)	Ruddy Turnstone	3.5 (4)
	Red Knot	5.3 (6)
	Sanderling	53.5 (61)
	Dunlin	4.4 (5)
	Semipalmated Sandpiper	32.5 (37)
	Short-billed Dowitcher	0.9 (1)
Dunlin (*Calidris alpina*)	Ruddy Turnstone	0.9 (1)
	Red Knot	1.5 (6)
	Sanderling	5.3 (21)
	Dunlin	3.5 (14)
	Semipalmated Plover	0.5 (2)
	Short-billed Dowitcher	0.5 (2)
Semipalmated Sandpiper (*Calidris pusilla*)	Semipalmated Plover	0.5 (2)
	Ruddy Turnstone	3.0 (12)
	Red Knot	1.5 (6)
	Sanderling	5.3 (21)
	Dunlin	3.5 (14)
	Semipalmated Sandpiper	85.6 (338)
	Short-billed Dowitcher	0.5 (2)
Short-billed Dowitcher (*Limnodromus griseus*)	Ruddy Turnstone	1.8 (1)
	Red Knot	3.5 (2)
	Sanderling	1.8 (1)
	Dunlin	12.3 (7)
	Semipalmated Sandpiper	5.3 (3)
	Short-billed Dowitcher	75.4 (43)

As the number of interspecific aggressive interactions was very low in Matts Landing, Bivalve and Thompson's Beach (n = 11), I applied this model only to data collected in Fortescue. I carried out all statistical analyses using statistical program R (R Development Core Team 2016). All means are presented as mean ± 1 SE.

RESULTS

I collected 209 scan videos that met specified multi-species criteria. The composition of mixed-species foraging flocks differed among study sites. Matts Landing, Bivalve, and Thompson's Beach were dominated by Dunlins, sandpipers and dowitchers, with a smaller proportion of Greater Yellowlegs (*Tringa melanoleuca*) and Lesser Yellowlegs (*T. flavipes*) at the beginning of migration period. Semipalmated Plovers (*Charadirus semipalmatus*) and Black-bellied Plovers (*Pluvialis squatarola*) joined the foraging flocks as the season progressed. In Fortescue, besides Dunlins, sandpipers and dowitchers, additional species found were turnstones, knots and Sanderlings.

On four study locations, I recorded 1,447 aggressive, 1,031 intraspecific and 416 interspecific interactions. The number of in-

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traspecific aggressive interactions per flock was significantly higher (4.93 ± 0.54, Range = 0-53), compared to interspecific interactions (1.99 ± 0.25, Range = 0-24, $P < 0.001$). Accordingly, 71.2% of all observed interactions were intraspecific (Tables 2 and 3). The most aggression to heterospecifics was exhibited by Sanderlings that often attacked sandpipers (32.5% of events) (Table 2). Considering all recorded interspecific interactions, significantly more aggression was directed toward smaller than similarly sized or larger competitors ($P < 0.001$); 67.2% of attacks was directed toward birds smaller than the attacker, 14.7% were directed toward similarly sized competitors, and 18.1% of interactions were directed toward larger competitors. In addition, attackers were winners of 95.2% of intraspecific and 99.0% of interspecific contests. When the attacker was larger than defender, 99.6% encounters were won, 100.0% when the attacker was similarly sized as defender, and 96.2% encounters were won by a smaller attacker ($P < 0.001$).

Differences in per-capita rates of aggressive interactions were significant among all pairs of species (for all species pairs $P < 0.01$), except knots to Sanderlings ($P = 0.37$), Dunlins to dowitchers ($P = 0.51$), sandpipers to knots ($P = 0.16$), and sandpipers to Sanderlings ($P = 0.71$) (Fig. 1). The highest rate was recorded in turnstones (0.13 ± 0.01), while the least aggressive were Dunlins (0.005 ± 0.001).

According to the negative binomial GLMM applied to the data set from Fortescue, per-capita rates of interspecific interactions were higher when the proportion of Sanderlings ($P < 0.001$), knots ($P < 0.01$), and turnstones ($P < 0.01$) was higher. To validate the fit of the model, I plotted the Pearson residuals vs. the fitted values and model's covariates. In addition, to evaluate whether there were residual patterns in these graphs, I modeled the Pearson residuals as a smoothing function of the model's covariates. Since the smoothers were not significant, I concluded that there were no patterns in residuals and that the model described the observed data well (Zuur and Ieno 2016).

DISCUSSION

In the Delaware Bay, shorebirds exhibited a higher level of aggression toward conspecifics than toward members of other species, which is consistent with previous studies (Kalejta-Summers 2002). Intraspecific interactions were more aggressive compared to interspecific ones; fights and chases were common among conspecifics, while heterospecific interactions were mainly supplanting attacks. During the breeding season, intraspecific aggression is associated with acquisition of nest sites, mates and food, while interspecific aggression is related to defense of nest sites and food (Peiman and Robinson 2010). However, during stopovers both conspecific and heterospecific individuals most likely compete over food and/or foraging space (Colwell 2000), as birds have a relatively short period to replenish energy before continuing their migration to northern breeding areas (Colwell 2010). Metcalfe and Furness (1987) suggested that foraging shorebirds obtain access to food through intraspecific aggressive interactions and keep spacing through interspecific aggression. In Delaware Bay, this pattern may not be true for individuals that foraged at Fortescue. Along sandy beaches, shorebirds feed on horseshoe crab (*Limulus polyphemus*) eggs either in a swash zone, where eggs were scattered on the top of sand surface by wave action (Botton *et al.* 1994), or they feed on eggs concentrated in crab nests, over which

Table 3. Proportions (%) of conspecific and heterospecific aggressive acts.

Aggressive Acts	Threat Display	Displacement Without Poking or Hitting	Poking or Hitting	Chasing	Fight
Conspecific	80.0	66.5	68.6	86.2	100.0
Heterospecific	20.0	33.5	31.4	13.8	0.0

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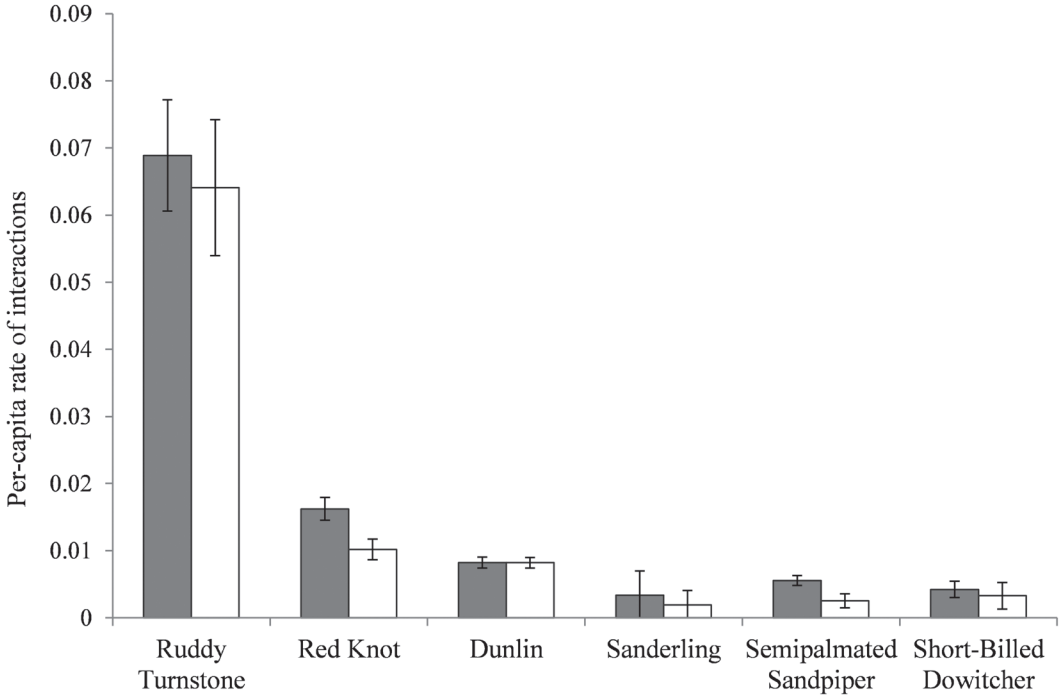


Figure 1. Interspecific differences in mean per-capita rates of intraspecific aggressive interactions (± SE) (gray bars) and mean per-capita rates of interspecific aggressive interactions (± SE) (white bars).

multiple species actively compete for access to food (Myers 1986). At Fortescue, the density of foraging birds around crab nests was very high, exceeding 50 birds per m^2 (Novcic 2014), and aggression was aimed at deterring competitors from the nests rather than keeping spacing among foragers.

Even though I observed more intraspecific interactions, the incidence of interspecific interactions was higher than previously reported for shorebirds, particularly at Fortescue where 30% of aggressive interactions were among heterospecifics. In mixed-species foraging assemblages, interspecific dominance relationships may be established, which can have a strong influence on individual behavior (Daily and Ehrlich 1994). Members of a dominant species, through interspecific social dominance, gain access to resources as they are successful in supplanting subordinate species (Martin *et al.* 2017). Dominant species are usually larger than subordinate ones, as aggression toward smaller-sized species is more profitable because it is easier to displace smaller ones than those of similar size (Daily and Ehrlich 1994). Thus, it is not surprising that the majority of attacks were directed toward smaller foragers, like sandpipers, the smallest and most abundant constituents of mixed-species foraging flocks.

Due to differences in the size of competitors, heterospecific interactions are commonly asymmetric, when one species is repeatedly dominant over the other species. Martin *et al.* (2017) found that 80% of 270 species pairs, across various avian taxa, contained dominant species that won over 80% of aggressive encounters, and, for the majority of species pairs, the dominant species was larger than the subordinate one. For shorebirds in Delaware Bay, the sample size was insufficient to examine dominance relationships for each species pair, but I found that attackers won 99% of interspecific encounters. Given that the majority of interactions was initiated by a larger competitor, it is clear that larger species dominated smaller ones on foraging sites. Nevertheless, almost all interactions initiated by smaller species were won as well, suggesting that smaller species

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were able to displace larger competitors and thus benefit by gaining access to resources.

This study indicates that per-capita rates of aggressive interactions depend on the flock composition, with turnstones, knots and Sanderlings being positive predictors of heterospecific interactions. This finding is not surprising as the highest per-capita rates of aggression, among all observed species, were recorded in turnstones. Horseshoe crab eggs buried beyond the reach of sandpipers are frequently brought to the surface by turnstones (Myers 1986), attracting large numbers of shorebirds around excavated crab nests, and eliciting aggression of turnstones. Even though the majority of agonistic interactions involving turnstones were intraspecific, turnstones also directed their aggression toward other species or were attacked by heterospecifics, including smaller shorebirds, such as Sanderlings and sandpipers.

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