Predator chases by breeding waders: interspecific comparison of three species nesting in Iceland

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Jónsson, J.E. & Gunnarsson, T.G. 2010. Predator chases by breeding waders: interspecific comparison of three species nesting in Iceland. *Wader Study Group Bull.* 117(3): 145–149.

Keywords: waders, shorebirds, mobbing, predator, nest defence, intrusions, Iceland, parental investment, body size

Parents defend their offspring from avian predators by distracting them with diversionary displays or drive them away by aggressive mobbing. The intensity of such defence can vary with the hazard that any given predator represents but also with characteristics of the mobber species. Decision making of parents in responding to different predators has potentially great fitness implications. We studied the responses of differently sized waders to different avian predators in south Iceland during 2001–2003. We collected data on *intrusions*, which we defined as the appearance of a predator within our study site. We compared mobber species with respect to location and predator (species, flight pattern and flight altitude). The most commonly observed mobbers were Black-tailed Godwit *Limosa limosa*, Whimbrel *Numenius phaeopus* and Redshank *Tringa totanus*, which performed 89.4% of all mobbing events. Four predators were the most commonly observed (93% of all intrusions), Common Raven *Corvus corax*, Arctic Skua *Stercorarius parasiticus*, Lesser Black-backed Gull *Larus fuscus* and Great Black-backed Gull *L. marinus*. Godwits and Whimbrels responded to the different predators with varying intensity but Redshanks responded similarly to the four predator species. We suggest that the size of predators and mobbers influences mobbing intensity in waders through mobber risk perception. Parental investment at different stages of the breeding season must take into account the differing presences of predators and will be dependent on predator breeding schedules.

INTRODUCTION

Parents can adjust their behaviour by trading off current reproductive success with possible future reproductive success (Clutton-Brock 1991). Protection of offspring in the form of nest or brood defence behaviour (hereafter mobbing) represents a mortality risk or energy expenditure that is offset by the survival of current offspring (Montgomerie & Weatherhead 1988, McLean & Rhodes 1991, Palestis 2005). In general, parents ignore predators, distract them with diversionary displays or drive them away by aggressive mobbing (Sordahl 2004).

Mobbing is costly and intensity of defence of nests and young should vary with the hazard that any given predator represents (Montgomerie & Weatherhead 1988, McLean & Rhodes 1991, Clode *et al.* 2000, Palestis 2005). Parents also adjust their defence in relation to variables that co-vary with parental investment, such as offspring age (Whittam & Leonard 2000, Sordahl 2004). Temporal variation in mobbing intensity can also be affected by breeding phase or changes in predation pressure. For example, young can escape predation or hide from predators on the ground whereas eggs are stationary (Pavel & Bures 2001, Palestis 2005, Pavel 2006). Furthermore, many birds are able to discriminate between predators that pose differing threats (Ydenberg & Dill 1986, McLean & Rhodes 1991, Sordahl 2004).

Life-history theory predicts that long-lived species with lower reproductive output should be more prone to avoid costs (such as risk of injury or depredation) when threatened by predators than shorter-lived species with higher reproductive output (Ackerman *et al.* 2006). In precocial birds, anti-predation behaviour is reported to be unaffected by brood size, contrary to that observed in altricial species (Sandercock 1994, Ruusila & Poysa 1998). Thus, anti-predation efforts are independent of offspring numbers when predators only take one offspring at a time, such as in precocial species, in which the young are able to disperse (Sandercock 1994). Nest defence is much studied in altricial species (Pavel & Bures 2001, Rytkonen 2002, Pavel 2006, Fontaine *et al.* 2007, Grim 2008), and in semi-precocial species such as terns and gulls (Shealer & Burger 1992, Clode *et al.* 2000, Whittam & Leonard 2000, Meehan & Nisbet 2002, Palestis 2005, Stenhouse *et al.* 2005), whereas such studies on precocial species with dispersing broods are less common (but see Sandercock 1994, Larsen *et al.* 1996, Ruusila & Poysa 1998). Thus, parental responses in precocial species can represent an all-or-nothing scenario, whereas parental response of altricial species is more likely to be a function of brood size.

We compared the mobbing behaviour of three wader species that are all common nesters in Iceland: Black-tailed Godwit *Limosa limosa* (hereafter Godwit), Whimbrel *Numenius phaeopus* and Redshank *Tringa totanus*. All these species lay a fixed clutch of four eggs (rarely three) per season. Re-nesting rates are probably low at this northerly latitude except for early failures. All three species brood their chicks when they are young and lead them to suitable feeding areas, but apart from that parental care is limited and mainly takes the form of predator defence. They all breed semi-colonially

in most areas of lowland Iceland (Gunnarsson *et al.* 2006a), and are aerial species that are conspicuous during the breeding season (Pullianen & Saari 1993, Gunnarsson 2000, Gunnarsson *et al.* 2006b). They are long lived birds with estimated annual adult survival rates of >90% for Whimbrels and Godwits (Grant 1991, Gunnarsson 2000, Gill *et al.* 2001) and around 80% for Redshank (Ottvall 2005, Burton *et al.* 2006).

Body-size influences many types of animal behaviour, such as foraging, fighting, fleeing, danger perception, risk assessment, family maintenance and interactions with other individuals (Dial *et al.* 2008, Jónsson & Afton 2009). The body-size of predators influences responses by defending parents (Templeton *et al.* 2005, Soard & Ritchison 2009). Moller (2009) reported a positive correlation between flight initiation distance (distance between predator and prey when escape begins) and basal metabolic rate in birds. He hypothesized that larger species were more likely to take risks because of their higher basal metabolic rate, which correlates strongly with body-size (McKechnie *et al.* 2006, McNab 2009). Similarly, we hypothesized that body-size affects the risk assessment of parents with respect to incoming predators, although this particular risk assessment is not directly comparable to that for flight initiation distance. In this instance, we consider that smaller species are more at risk from injury when mobbing a large predator than a larger species mobbing the same predator. Thus, we predicted that (1) the smallest species, Redshank, would be less likely to mob the largest predators; and (2) that the largest species, Whimbrel, would be the most likely to mob all predators.

Our objective was to compare mobbing intensity between species with respect to the intruding predator species. We defined mobbing intensity as number of mobbing individuals of each mobber species against a given predator species. We collected data on *intrusions*, which we defined as the appearance of a predator within our study site, regardless of whether it elicited a response from mobbers or not. We defined chase responses from mobbers as mobbing events, i.e. the event when an individual took flight and actively chased an incoming predator.

METHODS

Study area and habitats

The data were collected on nine study sites in the lowlands of S Iceland between 2001 and 2003 (e.g. Gunnarsson *et al.* 2005) distributed 2 to 40 km from the coast. The two habitat types considered here were dwarf-birch bogs (4 sites) and marshes (5 sites) where Godwit density ranged between 20 and 30 pairs/km^2 (Gunnarsson *et al.* 2005). The sites ranged in size between 25 and 200 ha and the spacing between the sites that were furthest apart was *c.*40 km. The sites had similar breeding densities of Whimbrels and Redshanks (10–15 pairs/km^2). Godwits and Whimbrels have the same modal starting date of incubation in Iceland (around 31 May) (Gunnarsson 2010) and smaller sample sizes for Redshank suggest they are on a similar schedule (Davidsdottir 2010). Other species of waders breed on most of the study sites but they are infrequent mobbers compared with the species under study. These are mainly Eurasian Golden Plover *Pluvialis apricaria* and Common Snipe *Gallinago gallinago*; both species use diversionary displays against threats rather than mobbing.

Predator intrusions were recorded on twice-weekly daytime visits to the study sites between 1 May until 20 July, and all observed intrusions were recorded. All the study sites are in open habitats where avian predators are very unlikely to be missed by the observer, and certainly not in any systematic way. The location of the observer when data were collected varied randomly and we do not consider that it would have affected the behaviour of birds in a systematic manner.

Data collection

Over the course of the three summers, we recorded 253 intrusions. In 222 intrusions (87.7%) intruding predators were solitary. Thus, we did not attempt to analyze effects of number of predators.

For each intrusion, we recorded date, time and: (1) species and number of intruding predators, maximum and minimum flight altitude of predators (in m); and (2) species and number of mobbers. We compared the mobbing frequencies of the three most common mobbing species against predators, with respect to the predators' flight patterns (undulating or straight) and flight altitudes. Flight pattern and flight altitude may signal the intent of avian predators, i.e. high, straight flying individuals may be passing through the area rather than searching for prey. Undulating flight occurred especially when it was evident that some predators (particularly Arctic Skuas *Stercorarius parasiticus*) were actively searching for prey. When predators varied their altitude during intrusions, both max and min altitudes were recorded. Observations were made with binoculars (8×) or the naked eye (if close) and altitudes and flight patterns were estimated visually.

Species of mobbers were Godwit, Whimbrel and Redshank, but also Eurasian Oystercatcher *Haematopus ostralegus*, Dunlin *Calidris alpina*, Arctic Tern *Sterna paradisea*, Black-headed Gull *Larus ridibundus*, Arctic Skua, Redwing *Turdus iliacus* and Meadow Pipit *Anthus pratensis*.

Species of predator were Merlin *Falco columbarius,* Short-eared Owl *Asio flammeus*, Lesser Black-backed Gull *L. fuscus*, Great Black-backed Gull *L. marinus*, Black-headed Gull, Arctic Skua, and Common Raven *Corvus corax*.

In Iceland, Common Ravens initiate breeding in April, Lesser Black-backed Gulls in late May or early June, Arctic Skuas in the last week of May or early June, and Great Black-backed Gulls in late April or early May (Petersen 1998). Therefore, their appearances were temporally restricted, and seemed to coincide with the period when they are providing food for their young. Common Ravens were mostly observed in May (78% of all Common Raven intrusions), with all of the remaining observations occurring in June. All intrusions by Great Black-backed Gulls were observed in July, whereas those of Arctic Skuas were all seen in June. Lesser Black-backed Gulls were observed in June (71%) and July (29%). Thus, month and predator species were confounding variables, at least for Common Raven, Great Black-backed Gull and Arctic Skuas. Therefore we opted to compare mobbing with respect to predator species, while considering their differential occurrence over time in the interpretation of the findings.

Data analysis

We used number of mobbers, within each mobber species, as a measure of mobbing intensity in the interspecific comparison we present here. By virtue of 24 hour daylight in Iceland at the time of observations, predators and mobbers were clearly visible at all times.

Mobbing intensity

We compared mobbing intensity (number of individual mobbers of one species, given a predator species) between mobbers with generalized linear models (PROC GENMOD; SAS Institute 2001), using log link and the Poisson distribution (Agresti 1996). If one intrusion yielded more than one mobbing species, that intrusion was included for all mobber species in question.

We ran three Poisson regressions, where number of mobbers was the response variable: Godwit (n = 108 mobbing events), Whimbrel (n = 103 mobbing events), and Redshank (n = 60 mobbing events). Predator species (Arctic Skua, Lesser Black-backed Gull, Great Black-backed Gull, and Common Raven) was a categorical explanatory variable. Other response variables were (1) lowest flight altitude of each predator during a given observation, as estimated by the observer; (2) flight patterns of intruding predators (undulating or straight), as determined by the observer, and (3) study site to account for unmeasured difference between sites.

Goodness of fit of all models was estimated and adjusted with the Pearson scaling factor if needed (Stokes *et al.* 2000 p. 360). We used backwards stepwise model selection with a Type 3 Likelihood ratio test (LR test) to determine final models and used only models with significant main effects to calculate parameter estimates. We used $\alpha = 0.05$ as the significance level in statistical tests. We used a post-hoc comparison of least-square means (hereafter LS means) with our LR test to compare number of mobbers for each predator.

RESULTS

The most commonly observed mobbers were Godwit, Whimbrel, and Redshank, which performed 89.4% of all mobbing events. Four predators were the most commonly observed (93% of all intrusions): Common Raven, Arctic Skua, Lesser Black-backed Gull and Great Black-backed Gull. Data on these predator species were analyzed for each individually but the remaining avian predator species (a total of n = 19 mobbing events) were used as a reference category (the choice of which is arbitrary) for analysis of mobbing intensity of each mobber species.

Mobbing intensity

Black-tailed Godwit

Godwits responded with varying intensity to predator species but responded similarly with respect to other variables. The LR test indicated that the number of mobbing Godwits was affected by predator species ($F_{3,164} = 7.94$, $P < 0.0001$) but was not related to location ($F_{8,164} = 0.91$, $P = 0.51$), predator flight altitude ($F_{1,164} = 0.01$, $P = 0.98$) or predator flight pattern ($F_{1,164} = 1.98$, $P = 0.16$).

LS means indicated that Godwits mobbed Common Ravens less often than either Arctic Skuas (estimate = –1.23, SE = 0.41, $\chi^2 = 9.1$, $P = 0.0025$) or Lesser Black-backed Gulls (estimate = –1.53, SE = 0.40, $\chi^2 = 14{,}7$, $P = 0.0001$), whereas there were no differences between the frequency with which they mobbed Arctic Skuas, Lesser Black-backed Gulls and Great Black-backed Gulls ($P > 0.05$).

Whimbrel

Whimbrels responded differently to different predator species and in different locations but responded similarly with respect to other variables. The LR test indicated that the number of Whimbrel mobbers was unaffected by predator flight pattern ($F_{1,164} = 0.01$, $P = 0.99$) or predator flight altitude ($F_{1,164} = 0.10$, $P = 0.76$), but was significantly related to predator species ($F_{3,164} = 5.10$, $P = 0.0021$) and location ($F_{8,164} = 3.11$, $P = 0.0027$).

LS means indicated that Whimbrels mobbed Common Ravens more often than Arctic Skuas (estimate = 0.97, SE = 0.34, $\chi^2 = 8.1$, $P = 0.0044$), and mobbed Arctic Skuas (estimate = –1.40, SE = 0.39), $\chi^2 = 12.5$, $P = 0.0004$) and Lesser Black-backed Gulls (estimate = –1.0, SE = 0.37), $\chi^2 = 7.5$, $P = 0.0045$) less often than Great Black-backed Gulls. There were no differences between the frequency with which Whimbrels mobbed Common Ravens and the two gull species or between the frequency with which they mobbed Arctic Skuas and Lesser Black-backed Gulls ($P > 0.05$).

LS means indicated that Whimbrels mobbed more often in Austurey than in five of eight of the other locations and more often in Kaldadarnes than in five of eight of the other locations($P < 0.05$). Mobbing intensity at Kaldadarnes and Austurey did not differ from one another and other locations did not differ in Whimbrel mobbings unless in relation to those two locations ($P > 0.05$).

Redshank

Redshank responded similarly in different locations and to predators of different species, with different flight patterns or flight altitude. No Redshanks were observed at Vatnsholt (n = 21 intrusions), and thus, this location was not included in the analysis for this species. The LR test indicated that the number of Redshank mobbers was unaffected by predator species ($F_{3,152} = 1.9$, $P = 0.14$), location ($F_{7,152} = 1.53$, $P = 0.17$), predator flight pattern ($F_{1,152} = 0.30$, $P = 0.59$) and predator flight altitude ($F_{1,152} = 1.9$, $P = 0.17$).

Body size of predator and mobber response

Godwits were more likely to mob the two smaller predator species, Arctic Skua and Lesser Black-backed Gull, than the two larger ones, Common Raven and Great Black-backed Gull (Fig. 1). The mobbing intensity of Whimbrels ranked positively with body size from the smallest to the largest; Whimbrels were more likely to mob the larger two species than the smaller two species (Fig 1). Redshanks responded similarly to all predators, except that they showed a slight, non-significant, tendency to mob Great Black-backed Gulls less frequently (Fig. 1).

DISCUSSION

The two larger wader species, Godwit and Whimbrel, responded differently to different predator species, whereas Redshank response was broadly similar for all four. Godwits were less likely to mob Common Ravens and Great Black-backed Gulls than other predators. Whimbrels were more likely to mob Great Black-backed Gulls than other predator species but seemed indifferent to Lesser Black-backed Gulls and Arctic Skuas. The flight altitude of predators, a potential indicator of threat, was apparently overridden by predator species and did not affect the response of any of the mobbers. Both of our predictions were fulfilled; i.e. that the smallest species was least likely to mob the larger predators and the largest species were most likely to do so.

We found that Godwits were less responsive to Common

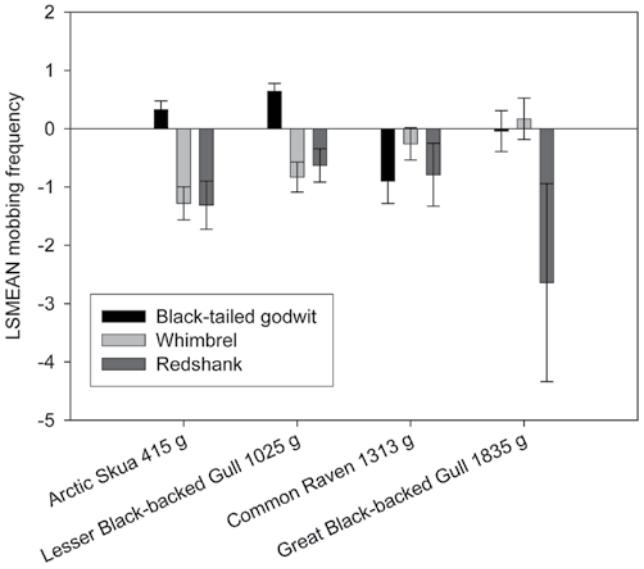

Fig. 1. Least-square mean (LSMEAN) mobbing frequency of three waders, grouped by the body size of the predator species, in Iceland 2001–2003. LSMEANS are calculated in PROC GENMOD, based on a reference category which was all of the other predator species observed (see text for details). Error bars are SE for each LSMEAN. Body masses of predators are medians calculated from ranges reported by Petersen 1998.

Ravens than other predators. Similarly, Bar-tailed Godwits *L. lapponica* are reported as being less responsive to Common Ravens than were Whimbrels (Larsen & Moldsvor 1992). Our findings in respect of Common Raven and Great Black-backed Gull were limited by the two predator species' activity over the study period. All Common Raven intrusions were recorded early in the study (May to the first week of June), whereas all Great Black-backed Gull intrusions were recorded in July. Common Ravens nest very early (April) but it was somewhat surprising that Great Black-backed Gulls were not observed in June. The finding that Godwits were unlikely to mob Common Ravens may relate to differences in Godwit activity between early nesting (Common Ravens present) and incubation and brood rearing (no Common Ravens recorded); i.e. Godwits were more active during the period that Common Ravens were absent because of their relative parental investment in each period of the nesting cycle.

Of the three mobber species, Redshank was the only one that did not respond differently to predator species. Redshanks may have been less likely to mob Great Black-backed Gulls than other predators, but our sample sizes were too small to infer such a difference (indicated by large error bars for Redshank vs. Great Black-backed Gulls in Fig 1). Redshank is the smallest species (*c*.175 g, Petersen 1998) and therefore probably less able to fend off avian predators than Godwits or Whimbrels. Moreover some of the predator species, especially Arctic Skuas, are agile flyers and could probably inflict injury on a mobbing Redshank, whereas the larger Whimbrel and Godwit may face less risk.

For large waders, Arctic Skuas may be friend or foe, depending on the proximity of their nests (Gunnarsson 2001). Whimbrels and Arctic Skuas often nest in close proximity, and in such cases Whimbrels often ignore the skuas when close to their nests. Similarly Redshanks may occasionally benefit from other species nesting nearby for their own protection (Valle & Scarton 1999).

In our study sites, the three mobbing wader species nest close to one another and conceivably there is some interaction between them in responding to different predators. Particularly, it would not be inconsistent with our results if Redshanks varied their response according to that of the larger waders. However, this would be difficult to evaluate in our study sites because the larger waders are always present; we would need to include sites with only Redshanks and no larger species.

It would seem possible that the differences between the predator responses of Godwits and Whimbrels arise because of differences in the assessments they make of the risk that the predators pose. Our results give little support for the idea that it represents an active division of labour between the larger Whimbrels (average body mass, *c*.450 g, Gunnarsson 2000) and smaller Godwits (*c*.300 g, Gunnarsson *et al.* 2006b). Moreover nothing in our data supports the suggestion that Godwits relies on Whimbrels for nest protection, as reported for Whimbrels and Bar-tailed Godwits in Norway (Larsen & Moldsvor (1992).

We found that our index of mobbing intensity, i.e. number of mobbers, differed between mobber species with respect to predator species. Allometrically, smaller species should enjoy superior locomotor performance (quick acceleration and manoeuvrability) than larger species (Dial *et al.* 2008). Nevertheless, our findings indicate that the smaller species may be more careful, perhaps because of a difference in physical strength. We found:

1. That the mobbing frequency of the largest wader (Whimbrel) increased linearly with predator size whereas the smallest species (Redshank) did not differentiate predators by species;
2. That the intermediate-sized Godwits were more likely to mob the two smaller avian predators; and
3. That the smallest species, Redshank, was the least likely to mob avian predators.

We suggest that risk assessment by the mobbers, associated with the body size of both the predators and the mobbers, influences mobbing intensity. The phenology of predator presence and mobber breeding schedules were confounded in our data and this affects the robustness of our conclusions. Nevertheless our data on mobbing intensity are consistent across the three mobber species and highlight differences in their perception of their most commonly encountered foes. The risk of injury on contact may be greater for smaller species, but the costs and benefits of mobbing might also vary with size if smaller species are less likely to deter a given predator.

ACKNOWLEDGEMENTS

We thank Jennifer A. Gill and Piet van den Hout for helpful comments on previous drafts of the manuscript.

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