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Factors that affect detection of threats from food competitors within a group

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G. Beauchamp. Factors that affect detection of threats from food competitors within a group

Abstract: Early detection is crucial to avoid threats from predators and competitors.

Factors that affect threat detection have rarely been investigated in the context of food competition. I examined the ability to detect threats of displacement from feeding areas by competitors in flocks of staging semipalmated sandpipers *Calidris pusilla* (L., 1766). I predicted that targeted birds would be more likely to detect competitors attacking from the side or from the front rather than from behind because a blind area behind the head interferes with detection. Preening or sleeping birds in feeding areas might be less likely to detect attacks if such activities interfere with vigilance. If targeted birds maintain vigilance against attackers, attacks launched from further away should be detected more frequently since more time is available for detection. As predicted, attacks were detected less often when launched from behind and more often when launched from further away. The longest attacks were detected less often perhaps because birds relaxed their vigilance when neighbours were further away. The ability to detect threats did not vary with targeted bird activity. Several factors influence the ability to detect threats from food competitors providing us with a novel context in which to investigate threat detection.

Key words: aggression, *Calidris pusilla*, kleptoparasitism, semipalmated sandpiper, sensory ecology.

Introduction

Animals in many species interrupt their activities to monitor their surroundings. Such vigilance is important to detect predators early (Beauchamp 2015). The ability to visually detect predation threats is expected to vary with a host of factors including the type of activity performed by animals (Kaby and Lind 2003), their posture (Lima and Bednekoff 1999; Bednekoff and Lima 2005), and eye configuration (Fernández-Juricic 2012). Animals can also aim their vigilance at competitors eyeing their resources such as food or mates. Vigilance, in this case, is important to detect threatening individuals early and avoid aggressive displacements (Goss-Custard et al. 1999; Robinette and Ha 2001; Sirot et al. 2012).

Threat detection has rarely been investigated in the context of competition. This is unfortunate as resource competition would provide a novel system in which to investigate factors that affect threat detection. In addition, these factors might act differently during competition. Competitors, for instance, can target a specific individual at very close range, which might cause changes in vigilance strategies against such threats. Therefore, the determinants of threat detection could vary depending on the type of threats faced by foragers.

Conflicts over resources are frequent in many bird species (Brockmann and Barnard 1979). They can occur when targeted animals perform different activities and can be launched from areas that are more difficult to visually monitor due to particular eye configuration. This provides us with an opportunity to investigate factors that affect threat detection in the context of resource competition. I explored these issues in fall

staging semipalmated sandpipers (*Calidris pusilla* L. 1766) that often compete aggressively with one another over food (Harrington and Groves 1977; Tripp and Collazo 1997).

When the rising tide covers mudflats on which they feed, fall staging semipalmated sandpipers roost on the shore. As the tide recedes, sandpipers aggregate in large feeding flocks. At that time, sandpipers use one of two foraging modes to gather resources. In visual mode, sandpipers search for buried prey and the head is kept high above the sediments. In skimming mode, by contrast, sandpipers maintain a close contact between bill and sediments and ingest minute prey found at the surface (MacDonald et al. 2012; Beauchamp 2013). Skimming birds can be aggressively displaced from their food patches by nearby companions (Beauchamp 2014). During an aggressive displacement, an attacker rushes at another bird with neck feathers standing out in a ruff, wings half spread, and elevated tail (Hicklin and Gratto-Trevor 2010). Earlier work suggested that relatively low foraging success appears to motivate aggressive displacements (Beauchamp 2014).

An attack often involves direct body contact with the targeted bird. Otherwise, the targeted bird leaves hurriedly as the attacker approaches and avoids contact. In all cases, targeted birds abandon their food patches (no resource defense). I assume that an attack ends with body contact when the targeted bird fails to detect the approaching attacker. Since an attack always causes displacement, the targeted bird has nothing to gain by staying put and receiving a blow. Upon detection of an attacker, targeted birds

should thus move away as soon as possible to resume feeding elsewhere sooner and avoid a blow.

Sandpipers have laterally-placed eyes and a blind area behind the head (Martin and Piersma 2009). I predicted that targeted birds should detect attacks more frequently, and thus avoid contact more often, when those attacks originate from the side or the front rather than directly from the back where monitoring can be more difficult. In skimming flocks, most birds are foraging but they can also preen or rest. Performing these activities might interfere with the detection of threats (Rattenborg et al. 1999; Dominguez and Vidal 2007), in which case I predicted that detection would be less likely to occur during those activities. Foraging and other activities like preening or resting can be interrupted by vigilance bouts aimed at detecting threats (Beauchamp 2015). Classic vigilance theory implies that detection should be more likely for attacks launched from further away because vigilance is more likely to occur at one point or another during a longer attack (Pulliam 1973). The final prediction is that detection should occur more frequently when attack runs are longer.

Methods

I conducted the study from late July to early August in 2012, 2013, and 2015 during the peak of adult fall migration in the Shepody area of the upper Bay of Fundy, New Brunswick, Canada (45.73° N, 64.65° W). I monitored skimming flocks using a 60x digital camcorder for about two hours each day as the tide receded. Focusing on a particular individual in skimming flocks proved difficult due to high bird density and frequent movements. Instead, I zoomed in on a particular area of the flock so as to keep

about 10-20 birds in view and maintained the camcorder focused there for about one minute. After this time interval, I focused on another area of the flock and repeated this process until the flock departed. Given the large number of birds using the site every day (from 1 000 to 100 000), I assumed that repeated sampling of the same birds was unlikely.

Using the recorded video sequences, I monitored the birds present in the frame to detect attacks. I scored all the attacks that I detected in each flock. Occasionally, the same bird was involved in successive attacks, in which case I only scored the first attack to avoid pseudoreplication. For each attack, I determined whether the targeted bird was skimming or not at the time of the attack. Other activities like preening or resting were lumped because they occurred infrequently. I determined the direction of the attack from the perspective of the targeted bird. Most attacks occurred directly from behind in the sense that the direction of attack would bring the attacker directly at the tail end of the attacked bird. Other possible directions like the side or the front were lumped because they occurred infrequently.

The length of the attack was obtained by playing the video sequences frame by frame (1 frame = 33 ms). An attack began when the attacker started to run in the direction of the targeted bird and ended when the attacker made direct contact with the targeted bird or reached the spot formerly occupied by the targeted bird before its hurried departure. For ease of interpretation, attack duration was classified into three different categories with an approximately equal number of events for each: short (less than 0.7 s), medium (more than or equal to 0.7 s and less than 1.07 s), or long (longer

than or equal to 1.07 s). Finally, the outcome of the attack was scored as non-detected when the targeted bird failed to avoid contact or as detected when the targeted bird avoided contact.

I used a mixed logistic regression model with day as a random factor (to control for a possible correlation between attack outcomes on the same day) and year, attack direction (from behind or not), targeted bird activity (skimming or not) and run duration (short, medium or long) as fixed factors. The dependent variable was the outcome of the attack (detected or not). I also considered the interaction between year and the other independent variables to determine whether the effect of these variables varied yearly. Interaction terms were dropped from the final model when not statistically significant. Post-hoc tests were used to contrast pairs of means. Back-transformed least-squares means and 95% confidence intervals are provided below.

Results

The dataset consisted of 332 attacks. Median attack length was 0.87 s, ranging from 0.17 to 6.0 s. Birds directed their attacks at the back of their targets (81%) and occasionally the side (18%) or the front (1%). Attackers mostly targeted skimming birds (91%) and occasionally preening (8%) or sleeping birds (1%). Detection, which was inferred from contact avoidance, occurred in 32% of the attacks.

Odds of attack detection varied yearly ($\chi^2_2 = 7.5$, $p = 0.02$; fig. 1a), but showed no association with targeted bird activity at the time of attack ($\chi^2_1 = 0.1$, $p = 0.72$; fig. 1b). Attacks aimed at the back of the targeted birds were detected less often than those aimed at the side or the front ($\chi^2_1 = 9.4$, $p = 0.002$; fig. 1c). The length of the attack run

influenced detection in a non-linear fashion ($\chi^2_2 = 7.7$, $p = 0.02$; fig. 1d) with more detection for medium runs than for either short or long runs.

Discussion

As predicted, attackers that approached their targets directly from behind were detected less often. Attacks from behind benefit from the fact that birds like sandpipers with laterally placed eyes cannot easily monitor areas just behind them. A tendency to attack from behind was also noted in another shorebird species (Sirot et al. 2012). In another study, detection also took longer when birds were attacked by a mock predator from behind (Kaby and Lind 2003). These general trends could be tested with species with other eye configurations. Species with more forward facing eyes, for instance, might have even more difficulty in evading attacks from behind.

Targeted bird activity at the time of the attack was not associated with attack outcome. This suggests that preening or resting birds, when compared to skimming birds, are at no disadvantage when detecting threats from within the group. Preening birds are known to maintain vigilance in many species (Redpath 1988; Randler 2005; Dominguez and Vidal 2007), and it is perhaps the case that preening birds can monitor their surroundings to a certain extent even when involved with other attention-grabbing activities. Sleeping might interfere to a greater extent with vigilance than preening and detection could prove more difficult (Rattenborg et al. 1999). Unfortunately, few birds slept in skimming flocks and this prediction could not be evaluated here. Since the relative availability of birds performing different activities was not established in

skimming flocks, it is not possible to determine whether attackers preferentially targeted particular types of birds.

As predicted, detection became more likely when attack runs lasted longer. This is similar to the observation that attacks by predators are more successful when they tend to be shorter (Cresswell 1994). Surprisingly, the longest attacks were detected less often. If animals interrupt their activities to maintain vigilance, longer attacks should remain undetected less often (Pulliam 1973). Why would the longest attacks be more difficult to detect? One explanation is that longer attacks are correlated with larger inter-individual distances (lower bird density). In many species facing threats from competitors, vigilance is known to decrease when neighbours are further away (see review in (Beauchamp 2015)). I surmise that birds with relaxed vigilance in low density flocks are less likely to detect threats.

I investigated the effect of attack direction, targeted bird activity, and attack run duration. The fact that detection also varied on a yearly basis suggests that other factors can play a role in avoiding aggressive individuals. Future work could seek these other factors. Attacks within groups to appropriate resources are common in animals and provide a novel system in which to investigate factors that affect threat detection. The results presented here also suggest that threats from competitors might be treated differently from predation threats especially when attacks last longer. Data from other systems will be able to shed more light on the constraints that animals face when visually detecting threats from competitors.

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Fig. 1. Factors that influence the probability of detecting an attack in flocks of semipalmated sandpipers (*Calidris pusilla*) over three study years. Factors considered in the mixed logistic regression model included study year (A), activity of the targeted bird at the time of the attack (B), direction of attack (C), and attack run duration (D). Letters above bars refer to the results of post-hoc tests between pairs of means. Means with different letters were significantly different. Back-transformed means are plotted and errors bars show the 95% confidence intervals.

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Fig. 1
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