



Function and structure of vigilance in a gregarious species exposed to threats from predators and conspecifics



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Vigilance can be targeted at predators or competitors, but there has been little work on the factors that affect vigilance aimed at competitors, which is known as social vigilance, and how it should be structured to detect and avoid conspecific threats. Social vigilance might be expected to play an important role in foraging groups with frequent conflicts over resources. I examined social vigilance in skimming semipalmated sandpipers, *Calidris pusilla*, which exploit minute prey at the surface of the substrate using a head-down position that leaves them vulnerable to aggressive displacement by neighbours. Attacks over resources occurred frequently in skimming sandpipers. In these groups, vigilance increased when neighbours were closer, suggesting that close neighbours posed a threat and that vigilance has a non-negligible social component in skimming groups. The negative exponential distribution best fitted the empirical distribution of intervals between successive vigilance bouts during skimming. This type of distribution implies that a bout of vigilance is initiated at the same rate regardless of the time spent head down in the current skimming bout, a feature that would prevent would-be attackers from targeting sandpipers at times of predictable vulnerability. This study shows that the occurrence of threats from within the group can promote randomness in the temporal organization of vigilance.

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Vigilance represents a major component of antipredator defences in birds and mammals (Beauchamp, 2014c). Monitoring the surroundings for signs of danger can greatly increase the chances of detecting predators before it is too late to escape. Antipredator vigilance is adjusted to the perceived level of predation risk. For instance, prey animals close to obstacles that prevent the detection of predators are expected to invest more time in vigilance (Lazarus & Symonds, 1992). Vigilance research has also focused on the best way to partition time between bouts of vigilance and foraging. In particular, initiating bouts of vigilance at regular or random intervals while foraging may be best suited to detect and avoid predators with different attack modes (Bednekoff & Lima, 2002; Scannell, Roberts, & Lazarus, 2001; Sirot & Pays, 2011).

While predators represent an obvious target of vigilance, potential rivals and foes from the same species have long been recognized as alternative targets (Hall, 1960; Jenkins, 1944). Monitoring rivals, also known as social vigilance, allows individuals to detect and assess potentially threatening situations (Cameron & Du Toit, 2005; Hirsch, 2002; Öst, Jaatinen, & Steele, 2007; Pangle & Holekamp, 2010; Treves, 1999). Interestingly, several ecological factors affect antipredator and social vigilance differently

(Beauchamp, 2015). For example, antipredator vigilance is expected to decrease in larger groups because numerous neighbours can help to detect threats more efficiently and dilute predation risk (Elgar, 1989). By contrast, social vigilance is expected to increase in larger groups with more opportunities for conflict (Beauchamp, 2001). Similarly, closer neighbours increase social risk by decreasing the reaction time of the targeted animals but decrease predation risk by providing layers of protection against predators (Hamilton, 1971) and better information about perceived threats (Lima & Zollner, 1996).

Unfortunately, antipredator and social vigilance are difficult to distinguish because animals often provide few clues about the target of their vigilance. This is especially the case for species with laterally placed eyes in which head orientation provides little information about the intended target (Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014; Dawkins, 2002). In view of the contrasting effect of several ecological factors on the two types of vigilance, pooling antipredator and social vigilance may be a poor choice to examine their effects. Isolating social vigilance is possible in some cases. In species with forward eyes, head orientation can provide a reliable clue as to the target of vigilance (Favreau, Goldizen, & Pays, 2010; Hirsch, 2002). In other cases, the context during which vigilance occurs, say, during the reproduction season

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(Klose, Welbergen, Goldizen, & Kalko, 2009) or when individuals fight over resources (Injaian & Tibbetts, 2015; Pangle & Holekamp, 2010), can also help pinpoint the target of vigilance.

Beyond the general intuition that social vigilance should increase when conspecifics pose a greater threat and that vigilance can help avoid threatening conspecifics (Goss-Custard, Cayford, & Lea, 1999), little is known about how such vigilance should be organized. For instance, should vulnerable individuals scan at regular intervals or in a more random fashion to monitor neighbours? There is a need to uncover study systems in which social vigilance plays an important role. In such a system, it will be possible to examine the factors that influence social vigilance and to determine how this type of vigilance is structured to allow detection and avoidance of threats from within the group. I investigated vigilance in a novel study system to determine the extent to which vigilance is aimed at competitors and how this type of vigilance is structured.

STUDY SYSTEM

I studied vigilance in a gregarious shorebird, the semipalmated sandpiper, *Calidris pusilla*. The study was conducted from late July to early August in 2012 and 2013 during the peak of adult autumn migration in the Shepody area of the upper Bay of Fundy, New Brunswick, Canada (45.73°N, 64.65°W). Mudflats where sandpipers forage are bordered by a salt marsh beyond which a thick forest cover extends 50–100 m away. Falcons (mostly *Falco peregrinus*) use the forest cover to hide their swift attacks on roosting or foraging sandpipers (Beauchamp, 2008; Dekker, Dekker, Christie, & Ydenberg, 2011; Sprague, Hamilton, & Diamond, 2008).

When the rising tide covers the mudflats, sandpipers roost on the shore. As the tide recedes, sandpipers aggregate in large feeding flocks near the tideline. The density in these flocks can initially be as high as 100 birds per square metre. At that time, sandpipers use one of two foraging modes to gather resources. In visual mode, sandpipers search for buried prey by looking down at a slight angle from the horizontal, but the head is kept high above the sediments. In skimming mode, by contrast, sandpipers maintain a close contact between the bill and sediments so that the head is directly pointing down. During skimming, birds ingest minute prey found at the surface (MacDonald, Ginn, & Hamilton, 2012). Skimming birds are frequently displaced from their patches by nearby companions (Beauchamp, 2014b). From the head-down position, sandpipers at times interrupt skimming to scan their surroundings. In the first part of the paper, I aimed to determine whether sandpipers monitor their neighbours during such scans.

PART 1: DO SANDPIPERS MONITOR THEIR NEIGHBOURS DURING SKIMMING?

Rationale and Predictions

In a vulnerable position when skimming head down, sandpipers might use vigilance to detect threatening neighbours. This is especially important in species like sandpipers with an extensive blind area behind the head (about 35° in width; Martin & Piersma, 2009). If vigilance has a social component in skimming flocks, I predicted that interscan duration, the length of time between two successive bouts of vigilance, would decrease rather than increase when neighbours were closer and require more monitoring (Hirsch, 2002; Treves, 1998). Here, I focused on interscan intervals because vigilance bouts were typically very short (median = 0.5 s) and insensitive to the various ecological factors assessed here.

Vigilance might be initiated for reasons unrelated to competition or predation. In particular, vigilance might be used to locate

alternative patches following local resource depletion (Krebs, 1974). If depletion plays a part in vigilance during skimming, I predicted that interscan duration would become shorter the longer a flock spent foraging. Depletion could also occur over several consecutive days of resource exploitation, in which case interscan duration should also become shorter as autumn staging progresses.

Methods

Flock and focal sampling

Skimming flocks were monitored from various vantage points using a 60x digital camcorder for about 1 h each day as the tide receded. In nearly all cases, I managed to start data collection as soon as a flock landed in a particular area. It proved difficult to focus on a particular individual in skimming flocks due to high bird density and rapid movements. In skimming flocks, I thus zoomed in on a particular area of the flock so as to keep about 10 birds in view. I maintained the camera focused on this area for about 1 min. I then focused on another area of the flock and repeated the same process until the flock moved on. Repeated sampling of the same birds is unlikely given the large number of birds using the site every day (from 1000 to 100 000).

Focal sampling was performed later using the recorded video sequences. I selected focal birds haphazardly from those visible on the monitor. I followed each focal subject until it flew away or was lost from sight. A focal observation was discarded if it lasted less than 10 s. In the retained focal observations, fewer than 10% of interscan durations lasted more than 10 s (see below), which means that inclusion of the shorter focal observations had a minimum impact on the occurrence of long interscan durations. For each focal bird, I estimated the distance to the nearest two neighbours in bird-length units (one unit \approx 10 cm) at the beginning of the focal observation. Distance to obstructive cover was estimated with stakes positioned at known distances on the mudflat.

For each focal observation, I watched the video sequence frame by frame (1 frame = 0.033 s) and calculated the duration of each interscan interval. An interscan interval started when the bill of a focal bird touched the substrate and ended when the bird raised its head above its shoulders to start a scan. Head movements of smaller amplitude (typically just a few centimetres) were considered part of the skimming process. A more fully raised head probably allows birds to monitor a larger area, which would provide scans of a higher quality (Fernández-Jurcic, 2012).

I also noted the occurrence of all attacks aimed at, or performed by, the focal bird. An attack involved a rush at another bird with neck feathers standing out in a ruff, wings half spread, and an elevated tail (Hicklin & Gratto-Trevor, 2010). Attacks often involved direct body contact with the targeted bird. Otherwise, the targeted bird left hurriedly before contact. In all cases, the attacker managed to displace the targeted bird. In addition to the occurrence of attacks, I noted whether attacks included contact with the targeted bird and, if so, the direction from which the attacker came (from the back, front or side of the targeted bird).

Statistical analysis

The distribution of interscan durations proved highly skewed to the right. Thus, I used a nonlinear mixed model with gamma-distributed errors (Proc Nlmixed, SAS, v.9.4, Cary, NC, U.S.A.). The gamma distribution is well suited to model fat-tailed interscan duration distributions (Scannell et al., 2001). Bird ID was used a random factor to control for individual variation. The fixed factors in the model included nearest-neighbour distance, distance to protective cover, migration phenology and time in patch. Migration phenology represented the Julian date for a focal observation with 30 July considered day 1. Time in patch represented the number of

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