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On the perception of targeting by predators during attacks on socially feeding birds

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We examined the spatial perception of predator targeting by prey during simulated hawk attacks on house finch, *Carpodacus mexicanus*, flocks, with an overall goal of gaining insight into the targeting process itself. Predator targeting of specific prey during attacks determines how danger is distributed among group members, and thereby determines key aspects of the safety of feeding in groups, such as risk dilution and its relationship to antipredator vigilance. During the main experiment, a model hawk suddenly appeared at either 3 m or 9 m from finches feeding near protective cover. The 9 m attacks always caused nearly all birds to flee to cover. During 3 m attacks, only birds directly in the line of attack fled to cover; the other birds instead consistently flew nearly perpendicular to the attack and away from cover. These results suggest that most finches did not perceive themselves to be targeted for attack when the hawk appeared at close range; otherwise, all birds appeared to perceive themselves as potential targets. A second experiment demonstrated that information about predator targeting is derived from observation of the predator itself rather than the behaviour of flockmates in the direct line of attack. A third experiment demonstrated that distance to cover also influenced the birds' response to targeting; thus, reactions to apparent nontargeting were not simply a matter of moving away from the line of attack. The differential perception of targeting during an attack is probably a widespread phenomenon in social birds and other animals.

Animals are usually safer from predatory attack when in groups than when alone (Krause & Ruxton 2002). Such 'safety in numbers' is often described as resulting from the collective detection of attacks through vigilance and from the dilution of risk during attacks. Dilution of risk comes about whenever a predator is able to kill only a small portion of the group, and, therefore, a predator must choose its victims from a larger number of vulnerable prey (Krause & Ruxton 2002; Caro 2005). The dilution of risk has usually been posited in an extreme form with only one victim out of the entire group (see Bednekoff & Lima 1998), which applies to many vertebrate prey. The collective detection of predators within a group of prey (McNamara & Houston 1992; Lima 1995) reflects the idea that individuals are somehow warned about an attack detected by another group member (a 'detector'). Nondetectors receive important information through collective detection, but they may be at a substantial disadvantage in responding to the attack, initiating escape, or gaining information about the attack itself (Lima 1995; Cresswell et al. 2000; Sirot 2006; Beauchamp & Ruxton 2007). Collective detection thus exists but in an imperfect and ambiguous form that leaves nondetecting group members with less information about an attack, and thus at greater risk, than detectors. The vigilance-related implications of imperfect collective detection have received much theoretical attention (Packer & Abrams 1990; McNamara & Houston 1992; Proctor et al. 2001; Jackson & Ruxton 2006).

The behavioural consequences of imperfect collective detection and risk dilution depend critically on how and when predators target (or choose) potential victims during an attack. In fact, drawing a clear distinction between risk dilution and collective detection depends on the nature of the latter and predator targeting (Bednekoff & Lima 1998). Simply put, the classic view of risk dilution (one victim with all members equally vulnerable) implies perfect collective detection. Lacking such perfection, the distinction between collective detection (or vigilance more generally) and risk dilution becomes less clear the longer a predator waits to commit itself to a specific target during an attack. In some cases, vigilance levels and risk dilution are strongly interrelated and thus not easily distinguishable (Bednekoff & Lima 1998). The vigilance scanning process itself can also be greatly influenced by predator targeting

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(Scannell et al. 2001; Bednekoff & Lima 2002; Sirot & Touzalin 2009). Furthermore, the issue of what defines the physical limit of a group may also be related to predator targeting. If predators target stragglers or isolated individuals for attack (e.g. Quinn & Cresswell 2006), then the effective group size might be limited to animals that are in fairly close proximity (see also Fairbanks & Dobson 2007; Fernández-Juricic et al. 2007).

Targeting is essentially a predator driven phenomenon (see also Jackson et al. 2006; Beauchamp 2007), and thus not easily studied. In fact, little quantitative information is available on such matters. Predators probably often target individuals that are late to respond, which would correspond with targeting relatively late in the attack process (Bednekoff & Lima 1998). The work of FitzGibbon (1989) suggests that cheetahs target gazelles early in the attack process, as indicated by their tendency to stalk the less vigilant gazelles in a herd (see also Krause & Godin 1996). Such early targeting is suggested in other biological systems in which predators may attack either denser portions of groups (Beauchamp 2008a) or larger groups over smaller ones (Botham et al. 2005; see also Krause & Ruxton 2002). Thus, existing evidence suggests that predator targeting is present, but that it differs across combinations of predators and prey.

Only a few studies provide quantitative information on targeting by bird-eating raptors. Vigilance-related early targeting (as per FitzGibbon 1989) has not been implicated during attacks on shorebirds by sparrowhawks, *Accipiter nisus* (Cresswell et al. 2003). This lack of early targeting by *Accipiter* hawks is in keeping with their tendency not to have their prey in view as they approach the site of an attack (Roth & Lima 2003; Roth et al. 2006). On the other hand, Quinn & Cresswell (2006) suggested that sparrowhawks preferentially attack relatively isolated shorebirds, which suggests early targeting in some situations involving highly dispersed flocks. Interestingly, these isolated birds are likely to be the more vigilant birds (see also Caro 2005). In fact, Lazarus (1978) proposed that greater vigilance in the more easily targeted edge birds could explain the ubiquitous vigilance group size effect (Elgar 1989; Roberts 1996; Caro 2005; Beauchamp 2008b), since edge animals make up a decreasing proportion of the group as overall group size increases. This ‘edge effect’, however, does not appear to explain the group size effect itself (Bednekoff & Ritter 1994; Fairbanks & Dobson 2007; see also Proctor et al. 2006; Rieucau & Giraldeau 2009).

We examined the issue of predator targeting during attacks by taking the prey’s perspective on the matter. Specifically, using simulated attacks by a model *Accipiter* hawk targeted on a specific portion of a flock, we asked whether socially feeding house finches, *Carpodacus mexicanus*, behave as though they are targeted for attack by the hawk. We based our experimental design and expectations on our impression (from observing many natural attacks) that *Accipiter* hawks commit themselves to a given target before initiating the final attack run only when they can get very close to a flock before doing so. If the finches perceive targeting in this way, then the birds in the target zone of an attack initiated at close range should behave very differently from those on the periphery of the attack. On the other hand, an attack initiated more distantly might leave all finches vulnerable to targeting and thus more uniform in their response. Based on their tendency to flee directly into cover or away from cover and the line of attack, our results indicate that house finches perceive predator targeting in much this way. Our results also indicate that the perception of predator targeting is based on personal information about the path of the attacking hawk rather than information gained from the escape behaviour of flockmates. We present our study in a series of self-contained sections, describing each of three experiments, followed by a General discussion.

GENERAL METHODS

Species and Study Site

This study was conducted during the late portion of two consecutive winters, February–March 1998 and 1999. The study site was in an open, mowed area adjacent to mature forest and an early successional field approximately 9 km southwest of Terre Haute, Indiana, U.S.A. House finches had been attracted to this study site each winter for several years prior to this study, and approximately 250–300 routinely feed there each winter. These birds seem largely dependent on human-supplied food during the winter (they are not native to eastern North America), and apparently had few other places to feed in the rural and sparsely populated local landscape. The finches were fed safflower seeds throughout the winter, both at the experimental feeder (see below) and at the main feeder maintained about 50 m away from the study site proper. Food was removed from the main feeder during experimental sessions but was otherwise available in both feeders. This work was conducted under a protocol approved by the Institutional Animal Care and Use Committee of Indiana State University (97SL to S.L.L.).

A schematic view of the study site is provided in Fig. 1. The prominent features of the site were the hawk chute, feeder, protective cover and blind. The hawk chute was a large wooden frame covered by thick-mil, opaque black plastic sheeting. This structure hid the model hawk during its acceleration down a monofilament line towards the feeding finches. The rear of the chute was 3.1 m tall, the end closest to the feeder was 1.7 m tall, and the width was uniform at 1 m. The feeder-facing end of the chute was also covered with black plastic with the exception of a 0.3 × 1 m opening, centred 1.2 m above the ground, through which the hawk emerged. The finches could not see into this dark opening from the feeder, and thus the hawk model appeared suddenly during a simulated attack, much as a real hawk would during an ambush attack.

The hawk model was constructed from wood and proportioned and painted to resemble an adult male sharp-shinned hawk, *Accipiter striatus*, in the gliding position. On its back were positioned two small plastic pulleys on which it moved quietly and with little friction. This hawk model dropped along a monofilament ‘attack line’ starting 3.1 m above the ground and ending 20 m away at 1.2 m above the ground. Its speed at the end of the chute was approximately 5 m/s. A fine monofilament ‘positioning line’, placed perpendicular to the attack line, held the attack line down at a point that ensured that the hawk model exited the chute at the proper height without any movement of the attack line prior to the hawk’s exit. A small metal cutting edge was installed in the head of the hawk model to (silently) cut the positioning line as the hawk exited the chute. A ‘hawk attack’ made only a small amount of noise, which was masked by a similar sounding noise played continuously from a small speaker at the base of the chute. The model hawk was released mechanically from within the blind.

The attack distance was varied by removing the sides of the chute on the end closest to the feeder (Fig. 1). For instance, during experiment 1, the feeder was placed 3 m from the end of the chute. With the chute sides in place, the hawk appeared at an ‘attack distance’ of 3 m from the feeder. However, the attack distance could be increased by rolling up the plastic sides of the first 6 m of the chute to expose the attacking hawk model at an attack distance of 9 m from the nearest point on the feeder. In this chute configuration, the model hawk exited from a 0.3 × 1 m opening centred 1.5 m above the ground, with the attack line properly positioned with a monofilament line as before.