Does an opportunistic predator preferentially attack nonvigilant prey?

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The dilution effect as an antipredation behaviour is the main theoretical reason for grouping in animals and states that all individuals in a group have an equal risk of being predated if equally spaced from each other and the predator. Stalking predators, however, increase their chance of attack success by preferentially targeting nonvigilant individuals, potentially making relative vigilance rates in a group relatively important in determining predation compared with the dilution effect. Many predators, however, attack opportunistically without stalking, when targeting of nonvigilant individuals may be less likely, so that the dilution effect will then be a relatively more important antipredation reason for grouping. We tested whether an opportunistically hunting predator, the sparrowhawk, *Accipiter nisus*, preferentially attacked vigilant or feeding prey models presented in pairs. We found that sparrowhawks attacked vigilant and feeding mounts at similar frequencies. Our results suggest that individuals should prioritize maximizing group size or individual vigilance dependent on the type of predator from which they are at risk. When the most likely predator is a stalker, individuals should aim to have the highest vigilance levels in a group, and there may be relatively little selective advantage to being in the largest group. In contrast, if the most likely predator is an opportunist, then individuals should simply aim to be in the largest group and can also spend more time foraging without compromising predation risk. For most natural systems this will mean a trade-off between the two strategies dependent on the frequency of attack of each predator type.

One of the main antipredation benefits for animals in joining a group is that the probability of their being attacked and killed decreases. This 'dilution effect' (Hamilton 1971) assumes that as long as individuals in a group are equally spaced and at the same distance from the predator then they all have an equal probability of being targeted and killed during an attack (Vine 1971). Within real animal groups, however, this may not be the case because ability to escape from predators, which varies between individuals, may be more important than relative position. One factor that influences average escape ability is how much time an animal allocates to being vigilant for predators while foraging.

Feeding or nonvigilant animals react more slowly on attack by a predator (FitzGibbon 1989; Krause & Godin

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1996; Hilton et al. 1999) and slower reacting individuals are more likely to be killed on attack (FitzGibbon 1989; Krause & Godin 1996). Predators could, therefore, increase their probability of attack success by initially targeting and killing a nonvigilant individual. If this occurs, then the antipredation benefits that accrue from the dilution effect will depend on an individual's relative vigilance rate, as well as its group size. For example, a nonvigilant individual in a large group may be more at risk of attack than a vigilant individual in a small group, despite the dilution effect. Understanding the targeting behaviour of predators is therefore crucial to understanding the evolution of animal grouping and other antipredation behaviours (Lima 2002).

The few studies that have investigated predator targeting behaviour with respect to vigilance have considered only predator species that stalk and have time to assess carefully the vigilance rate of their intended prey prior to attack. Cheetahs, *Acinonyx jubatus*, preferentially target the gazelle, *Gazella thomsoni*, with the lowest vigilance rate of a pair closest to its line of approach (FitzGibbon

1989) and as a consequence preferentially target males that have on average lower vigilance rates (FitzGibbon 1990). Cichlids, *Aequidens pulcher*, preferentially target guppies, *Poecilia reticulata*, that are foraging or that have nonvigilant postures (Krause & Godin 1996). The preferential hunting by these species may then greatly reduce or even remove the effects of dilution of risk because the probability of being attacked and killed primarily depends on body posture rather than on group size. However, many predators hunt without stalking their prey (e.g. Fanshawe & FitzGibbon 1993; Parrish 1993; Cresswell 1996; Noë & Bshary 1997), and may not have time to select on the basis of vigilance behaviour. In this study we tested for the first time whether an opportunistic predator targets prey with respect to their vigilance posture and determined whether the dilution effect can, under certain circumstances, remain the main selective force for grouping.

We tested whether sparrowhawks, *Accipiter nisus*, preferentially attacked vigilant (head-up) or feeding (head-down) models of the same avian prey presented in pairs at an open site at Falsterbo, southern Sweden, where hundreds of sparrowhawks pass daily during migration. Although sparrowhawks may stalk prey in wooded habitats they also frequently hunt opportunistically in the open (Rudebeck 1950; Newton 1986; Cresswell 1996). At our study site, the habitat is open with scattered low bushes where migrating sparrowhawks hunt by flying close to the ground or the bushes where they usually encounter prey by chance (see Rudebeck 1950 for extensive descriptions of opportunistic hunting by migrating sparrowhawks at Falsterbo). Of 14 attacks of sparrowhawks on wild birds observed during this study in the immediate area of the mounts, all were open, opportunistic attacks from a sparrowhawk flying low along the beach (see Cresswell 1996 for attack type definitions). Although hunting sparrowhawks could maximize their hunting success by always targeting nonvigilant individuals, we predicted that they would not have time to do so when hunting opportunistically, simply because there could not be enough time to assess state of vigilance.

METHODS

We carried out the study between 4 September and 22 October 2001 at Falsterbo in Southern Sweden (55°23′N, 12°50′E). During the autumn period several thousand sparrowhawks pass through this narrow peninsula as they migrate southwestwards (Kjellén 1992) and, at peak passage times, can be regularly seen hunting along the beach (Rudebeck 1950).

We presented sparrowhawks with model prey birds in pairs connected to a camera trap according to the experimental design of Götmark & Unger (1994). Model prey were of two types. The first was stuffed 3-week-old chickens (60–80 g) from an old Swedish breed that closely resembles the natural type of red junglefowl, *Gallus gallus*. The chickens were obtained from Tovetorp Zoological Research Station and mounted by Bo Nilsson, Torslanda, Sweden, under licence of the local Swedish County Administration. The second prey type was a resin cast

model of a greenfinch, *Carduelis chloris*, painted to resemble a male. Models of each type were identical except that half were mounted in a head-up position to mimic a scanning wild bird and half were mounted in a head-down position to mimic a feeding bird (Fig. 1).

We set up a maximum of 19 pairs of models daily at over 50 locations on Falsterbo: after 12 September, model locations were kept constant each day and confined to an 800-m strip of beach at Nabben at the tip of Falsterbo. We put out chicken models each day except on rainy days when greenfinch models were used, because rain damaged the natural chicken mounts. The distance between the models within a pair was 0.85 m with a head-up model on one side and a head-down model on the other. The position of the head-up model in the pair was swapped each day and also after each attack (although this was not possible for four attacks that occurred within a few hours of another attack). Models were placed on inconspicuous flexible wires that bent when hit. The wires were attached to concealed wooden posts pushed into the ground so that both models were of identical height. We placed models in low vegetation, such as long grass, or, more typically, rose bushes so that they appeared to be perched on top of the vegetation at a height of between 0.5 and 1 m above the ground. Foliage around the models was trimmed so that both were considered to be equally conspicuous, although as each model was swapped to the other's position regularly, any biases from position and foliage were equalized. Pairs of models were between 30 and 100 m apart. Of the 14 observed hunts on wild birds during the study all sparrowhawks were flying along the beach at less than 1 m above the ground at the start of the attack. At this height pairs of models could have been encountered only at short range by a sparrowhawk, probably becoming visible at most only 20 m away.

Each pair of models was connected to a camera trap (Firststrike, www.tracksys.co.uk) that was developed according to our specification for the experiments. A tilt switch was placed at the base of the wire of each model so that any substantial vibration of the model (equivalent to being hit gently by us) would result in a digital photo being taken. Sparrowhawks and any other predators that attacked a model during the day were therefore photographed automatically. Photos could be taken only at 1-s intervals so the vibration from hitting the model reasonably hard usually resulted in only a single photo being taken. At the end of a sampling period (usually each evening, but also at approximately midday on peak passage days) the cameras were downloaded. Each morning we took a reference photo to help judge which model was hit and from which direction the attack took place. During October an analogue clock was placed in the field of view of each camera to help distinguish separate attacks.

Cameras and models were set for a total of 45 days, usually from 0700 to 1900 hours, but for shorter periods on some days for logistical reasons or because of bad weather. In total, chicken models were put out for 4979 h and greenfinch models for 1444 h. There were 68 attacks: 40 by sparrowhawks, 13 by kestrels, *Falco tinnunculus*, five

(a)

(b)

(c)

(d)
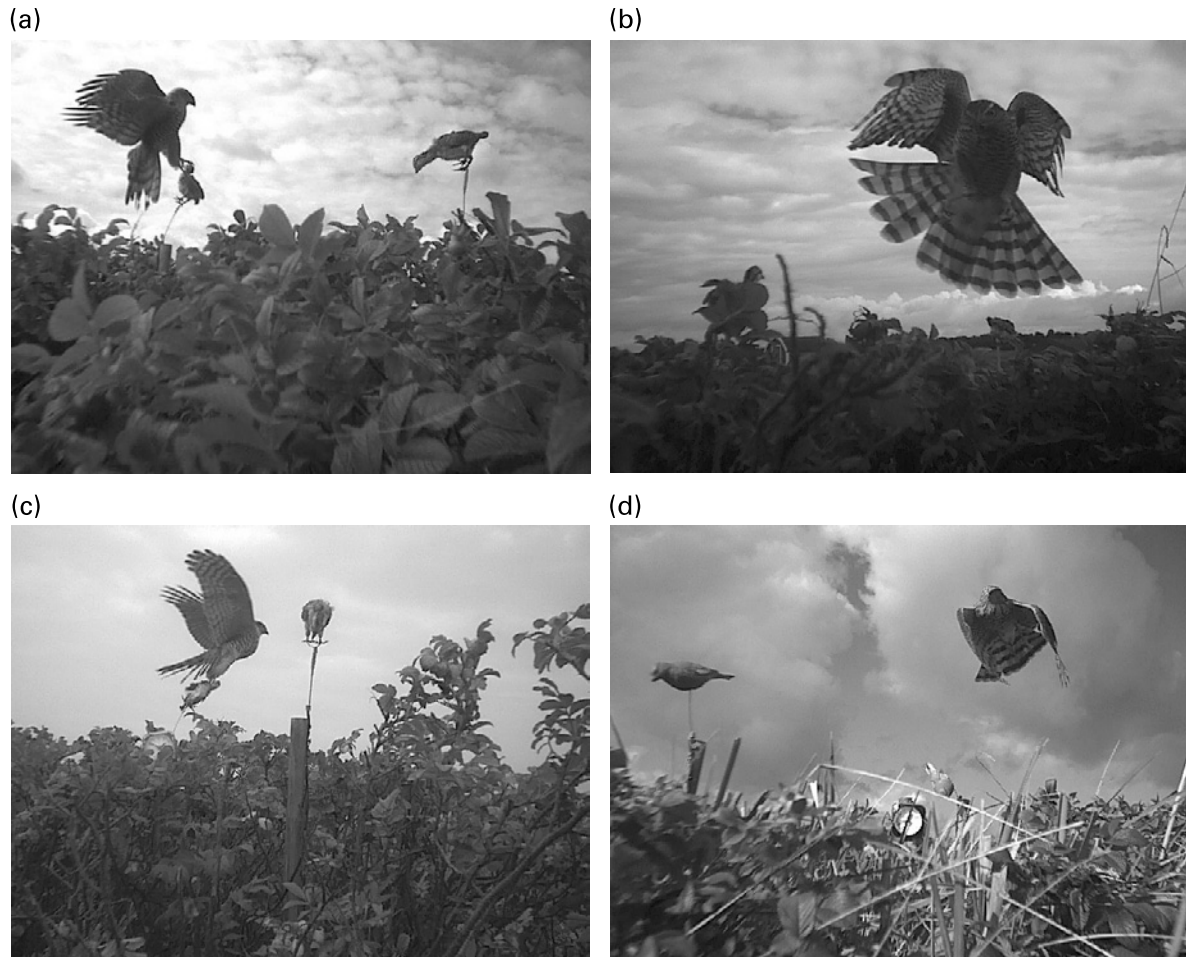
Figure 1. The photos of attack data demonstrate a number of important points in our methods and experimental approach. Two species were used as mounts (stuffed young chickens and model adult greenfinches), with each species put up in a pair with one in a head-down posture and the other in a head-up posture. As sparrowhawks were migrating through the study site it is likely that each attack was from a different sparrowhawk: plumage differences in these photos indicate that each attacking sparrowhawk was different. Changes in cloud patterns and including a clock in the field of view of the photo allowed us to identify any attacks on the same mount at the same time by the same sparrowhawk. Photos (c, d) show examples of where the approach direction of the sparrowhawk was obvious from the movement of the attacked mount, while (a) shows an example where attack direction could not be scored. Photos (b, d) show clearly how any movement of the mount indicated which mount was attacked in cases where the sparrowhawk was not photographed grabbing the mount.

by common buzzards, *Buteo buteo*, one by a rough-legged buzzard, *Buteo lagopus*, one by a great grey shrike, *Lanius excubitor*, two by magpies, *Pica pica*, and six were unknown (either unidentifiable because the photo was blurred or the predator was only partly captured by the photo). For this study we consider only data from sparrowhawks because sample sizes were too small for the other predator species. From each photo we determined which model had been attacked: in 42.5% of attacks ($N=40$) the sparrowhawk was photographed still holding on to the model and for the remainder the identity of the model that was attacked was clear because of movement of one of the models relative to the reference photo. A sparrowhawk sequentially attacked both models in only one case (the sparrowhawk attacked the second after perching on the first for several seconds); in this case data were used only from the first attack. For 25% of attacks more than one photo of the attacking sparrowhawk was

taken: in these cases it was clear that only one sparrowhawk was involved by reference to the time that the photo was taken or to the unchanging position and shape of clouds in the background. In 80% of attacks there was only one attack recorded by the camera between downloads. For the remaining four pairs of attacks we determined that the attacks were independent because the cloud pattern and light levels had changed markedly between photos.

Since the model targeted by sparrowhawks could be influenced by the order in which the models were encountered, we also classified attacks according to whether the model was closer to or further from the approaching sparrowhawk. We determined the direction of attack using the following rules. For birds perched on the models in the images, we used the direction that the sparrowhawks were facing and any bending of the model's wire from the attack. For images in which the

Table 1. Frequency of sparrowhawk attacks on models arranged in pairs (one in vigilant posture, the other feeding) with respect to their proximity to the approaching sparrowhawk

Position of model attacked with respect to approaching hawk	Vigilant	Feeding	Total
Four of five scored the same			
Further from hawk	6	6	12
Nearer to hawk	13	7	20
Three of five scored the same			
Further from hawk	7	8	15
Nearer to hawk	15	8	23
Overall all attacks	23	17	40

The results are given for cases in which approach directions of the sparrowhawks were scored the same by four of five observers and three of five observers.

hawk was no longer in contact with the models, we used the direction the sparrowhawk was facing in flight and the position of the mount attacked. All five of us scored the 40 attacks independently and were unanimous on 72%, with four of us agreeing on 80% of attack directions. We classified other attacks on the basis of the majority rule.

All statistical tests were exact probability tests calculated using SPSS (Norusĭs 1990). We carried out analyses on three data sets to determine if there were any effects on the experiment in our choice of location and because we used two model types: (1) all sparrowhawk attacks on all models ($N=40$); (2) all sparrowhawk attacks on chicken models only ($N=34$); (3) all sparrowhawk attacks at the single site, Nabben, on chicken models only ($N=33$).

RESULTS

Sparrowhawk attack frequency was independent of model posture: sparrowhawks attacked vigilant models on 57.5% of occasions ($N=40$, exact $P=0.43$). When attacks on greenfinch models were excluded, sparrowhawks attacked vigilant chicken models on 52.9% of occasions ($N=34$, exact $P=0.86$). When attacks on chicken models at Nabben alone were considered, sparrowhawks attacked vigilant models on 54.5% of occasions ($N=33$, exact $P=0.73$). Thus the result remains without the confounding effect of data from a second less realistic model type and a second site.

There was a slight trend for the model that was nearer the approaching sparrowhawk to be attacked more frequently than the model that was further away (62.5% of attacks, exact $P=0.19$, $N=32$ photos scored in the same way by four of us, Table 1). However, relative attack rates on vigilant and foraging models were independent of their proximity to the attack direction of the sparrowhawk (exact $P=0.47$, $N=32$ photos scored in the same way by four of us, Table 1). Results were similar if the larger sample size of photos scored in the same way by the majority of the five of us was used (Table 1). The slight trend for the model closer to the approaching hawk to be attacked is consistent with sparrowhawks hunting opportunistically.

DISCUSSION

Are Foraging Birds Preferentially Targeted?

Our data suggest that sparrowhawks hunting opportunistically do not target foraging prey preferentially. This is in marked contrast to other published studies that have shown a predator preference dependent on prey posture (FitzGibbon 1989, 1990; Krause & Godin 1996). However, both of these studies involved ambush predators that identify or stalk their prey in advance of attacking (cheetahs and cichlid fish), while sparrowhawks in our study area were clearly hunting opportunistically (unpublished data and see Rudebeck 1950). Thus our results suggest that the importance of differences in vigilance, or any other state-dependent factor, in determining targeting behaviour in predators depends on the mode of hunting. Predators in general may have time to discriminate between individuals on the basis of vigilance state only when stalking. Stalking is only one of many strategies used by predators generally and thus opportunistic hunting is an important type of predation to consider when investigating predation risk management in animal groups. Before discussing the implications of these findings for predation risk theory generally, we discuss whether our result could be due to limitations in our experimental design.

It could be argued that we did not find evidence for selection of feeding individuals because our experimental set-up did not realistically mimic a natural system (Slagsvold et al. 1995). This is unlikely because previous work using an identical type of model presentation system in a similar area has demonstrated strong preferences by attacking sparrowhawks (Götmark 1992, 1993, 1997; Götmark & Unger 1994) and consistent attacks even on pairs of models that deliberately did not mimic naturally encountered prey (Götmark 1994, 1996). Furthermore, although our sample size was relatively small, in part as a consequence of the fact that observing predation events by terrestrial vertebrate predators is rare, it was nevertheless almost twice as large as those obtained in other similar studies where selection by sparrowhawks for a variety of other traits was found (Götmark 1992, 1993; Götmark & Unger 1994). Thus lack of evidence from our study is unlikely to be caused by low power.

Whether a predator targets an individual according to vigilance state is likely to be also dependent on other factors and this could explain why we found no evidence for selection. Group size is one such factor because it is one of the main determinants of how soon a group detects an approaching predator (Pulliam 1973; Lazarus 1979; Cresswell 1994b). The larger the group the more important it is for the approaching predator to get as close as possible before being detected and thus the more important it should be to select individuals that are nonvigilant and likely to be slowest at responding. Conversely, in a small group, as represented in our experiment, it may be less important for predators to target individuals because the probability of detection or confusion (Neill & Cullen 1974) will be low in any case. Conspicuousness is another potentially confounding

factor. Our models were stationary and stationary feeding birds may be less likely to be detected by predators than moving ones. Thus if sparrowhawks were less likely to see our feeding birds because they were not moving, our effectively 50% attack rate on vigilant birds may mask an underlying selection for the feeding bird. Nevertheless, if this is the case, our results suggest that vigilance posture alone does not influence targeting behaviour.

Finally, another potentially influential factor could be spacing within flocks. On attack by sparrowhawks, non-vigilant redshanks, *Tringa totanus*, respond 0.07 s (median, range 0.05–0.12) slower than vigilant ones (Hilton et al. 1999). Stalking sparrowhawks attack at speeds of about 25 m/s (Hilton et al. 1999) and so for an attack where the sparrowhawk first sights the prey at a distance of 25 m, the relative difference in distance approached to either a vigilant or a feeding bird before being detected will be less than 2 m (7%). All other things being equal, nonvigilant prey under our experimental circumstances should therefore be easier to catch (Cresswell 1994a). However, because our models were only 0.85 m apart the difference in response times that might be expected by a sparrowhawk attacking real prey may be too small to make it worthwhile for the sparrowhawk to bother discriminating. Furthermore, if making a decision that is more complex than simply attacking any or the closest prey in a group involves a cost, for example by delaying the attack and thereby increasing the chance of being detected, then predators may target prey in a given vigilance state only if there is a large advantage to doing so.

Implications for Predation Risk Theory

If opportunistic predators do not preferentially target feeding animals in groups, the implications for predation risk theory are considerable. It implies that individuals should modify their grouping behaviour and behaviour within groups according to the type of predator they are most likely to encounter. When the most likely predator is a stalker, individuals should aim to have the highest vigilance levels in a group, rather than simply maximizing group size. For example, this might be the best strategy to adopt by small primates being hunted by the crowned hawk eagle, *Stephanoaetus coronatus*, a classic sit-and-wait predator of the African tropics (Zuberbühler 1997). In contrast, if the most likely predator is an opportunist, then individuals should simply aim to be in the largest group and can also spend more time foraging without compromising predation risk. For example, this might be the best strategy for ducks hunted by peregrines, *Falco peregrinus*, which make many open opportunistic attacks (Dekker 1980; Cresswell 1996). For prey that are likely to face risks from both predator types, for example redshanks which are hunted both opportunistically by peregrines and by stalking sparrowhawks (Cresswell 1993), the optimum strategy may be a trade-off between the two alternatives and dependent on the relative probability of being attacked by each predator type.

The results of our study and those involving stalking predators may then suggest that different hunting strategies of predators are a crucial component in determining the relative benefits of flocking because of reduced vigilance rates or the dilution effect. The general significance of nonselection on the basis of vigilance state is therefore partially dependent on how common opportunistic predators are. In sparrowhawks and similar hawk *Accipiter* spp. species worldwide, which prey on nearly all small bird species (del Hoyo et al. 1994), opportunistic hunting, where studied, is common (Rudebeck 1950; Goslow 1971; Newton 1986; Wilson & Weir 1989; Cresswell 1996). If opportunistic hunting is common then the predation risk to individuals in animal groups may be frequently independent of their own relative state of vigilance: this is perhaps to be expected given the widespread evidence that vigilance decreases with flock size (Elgar 1989). If there was a large cost associated with reduced vigilance in larger groups because of preferential targeting, then we would not expect such a universal decrease in individual vigilance rates with group size. Future research should, however, consider the different hunting strategies of predators when considering the benefits of the formation of groups as an antipredation strategy.

Overall, our data clearly suggest that opportunistic predators do not select prey in small groups on the basis of a vigilant or feeding posture alone. If preferential targeting does occur, we suggest it is likely to do so only under certain conditions (e.g. when prey are in larger groups) or on the basis of cues more complex than posture alone.

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