Ethology

The Use and Transfer of Information About Predation Risk in Flocks of Wintering Finches

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Abstract

Several studies in behavior have focused in some way on how groups of prey gather and use information about predation risk. Although asymmetries in information about risk exist among members of real groups, we know little about how such uneven information might affect individual or group antipredator decisions. Hence, we studied the use and transfer of information about the risk of predation in small flocks of wintering birds. House finches (*Carpodacus mexicanus*; 28 groups of three) were held in large enclosures divided into safe and risky patches. We controlled the information about risk available to each individual by conducting attacks with a model hawk that was visible to only a single (informed) bird. Repeated attacks on a single individual did not reduce the amount of feeding by other birds in that patch, although the time to resume feeding after observing a response to an attack event was somewhat longer than after a no attack event. These results suggest that informed individuals impart some information to naïve (uninformed) birds, but this effect was not strong. In fact, the frequent return of informed individuals to feeders after observing uninformed individuals feed suggests that finches relied more on public information regarding safety than their own personal information in deciding when to feed. Group patch choice appeared to be based on a majority-rules decision, although an effect of dominance status was apparent. Our results suggest that subordinate flock members may exert a large influence over group decision-making by acting as spatial 'anchors'.

Introduction

Many behaviorally complex organisms form groups (Krause & Ruxton 2002). The benefits of social living have been thoroughly reviewed (Krause & Ruxton 2002; Caro 2005) and include, but are not limited to, foraging benefits such as finding feeding locations (Clark & Mangel 1986; Valone 1989, 2007), reproductive benefits such as finding mates (e.g. Balmford 1991) and the social care of young (e.g. Clutton-Brock et al. 2000), and antipredator benefits such as shared vigilance and the dilution of risk (Elgar 1989; Dehn 1990; Lima 1995a,b). In all of these situations, information (whether about mates, feeding patches, or predation risk) is important to an individual in determining the costs and benefits of joining or leaving the group (Beauchamp & Fernandez-Juricic 2005; Jackson & Ruxton 2006). Moreover, many of these benefits of joining a group depend on the transfer of information within that group. For example, benefiting from the vigilance of other group members requires that these individuals share the information that they have detected a predator, either passively (e.g. by flushing) or actively (e.g. alarm calling). Thus, information transfer relieves information asymmetries among group members in a manner that is presumably adaptive for at least some of the individuals involved (Fernandez-Juricic et al. 2004; Dall et al. 2005).

Communication is the subject of vigorous research in behavioral ecology (Wiley 2006). A significant portion of this research has been devoted to communication about sex (e.g. Johansson & Jones 2007), with much less work devoted to predation risk. Information transfer about risk has been mainly limited to work in mammals (e.g. Deaner et al. 2005; Page & Ryan 2006; Hollen & Manser 2007; except for public information, Valone 2007) and fish (e.g. Hoare & Krause 2003; Kelley & Magurran 2003; Johnsson & Sundstrom 2007). In short, these studies have shown that information about risk obtained within a social context can influence an individual's behavioral decision making (see also Griffin 2004). Aside from the ground-breaking work by Fernandez-Juricic et al. (2004, 2006) and Fernandez-Juricic & Kacelnik (2004), work on the transfer of information about risk in birds is scant. While many theoretical and empirical studies have examined the costs and benefits of flocking, few have considered their dependence on information transfer (Conradt & Roper 2005; but see Jackson & Ruxton 2006).

One exception to this paucity of work on communication about predation is the study of alarm calls. Alarm calls are well known in parids and other species that maintain cohesive social flocks (Langham et al. 2006). These calls only occur during recent contact with a predator and likely act to inform the flock of immediate danger. Alarm calls may function in a game-theoretic 'diffusion of responsibility' manner (Taylor et al. 1990), have been shown to have mate guarding functions (Witkin & Ficken 1979), and recently have been found to contain information about the severity of the threat (Leavesley & Magrath 2005; Templeton et al. 2005) that may be transferable to other species in mixed species flocks (Magrath et al. 2007; Templeton & Greene 2007).

Still, we do not know if or how information about risk is transmitted by other means. Do less social species use alarm calls (or some audible equivalent)? Do birds use other, non-audible cues to transfer information about risk? What means besides personal vigilance do birds use to obtain information within a group? Moreover, we do not know how information transfer might translate into group decision making (Conradt & Roper 2005). This further elaboration is important because, although individuals collect information for themselves, they must often respond to stimuli and make decisions as a group. Group behavior is likely a compromise between the information-dependent behaviors of individual group members (Conradt & Roper 2005).

In this paper, we classify information into three categories: personal information, relayed social information (e.g. via a direct signal), and inadvertent social information (i.e. public information). There has recently been a great deal of discussion about the nature of the different types of information transfer, especially public information, and we refer the reader to Valone (2007), Dall et al. (2005), Dall (2005), and Danchin et al. (2004, 2005) for that debate. Here, we consider personal information as generally reliable in that it is obtained directly through an individual's own observation. However, the cost of acquiring this type of information can be high (e.g. obtaining information about predation risk through predator inspection; Milinski et al. 1997; Krama & Krams 2005). Less costly, and possibly less reliable, information can be obtained through information transfer from one individual to another. For example, an individual can obtain information about predator presence from alarm calls or other signals directed towards a presumed receiver even though the individual does not observe the predator directly (although such signals may sometimes be deceptive; Hauser & Nelson 1991; e.g. Tramer 1994; Ridley et al. 2007). Finally, information can be obtained through public information or the observation of other's behavioral cues without obvious, 'intentional' signaling. This third method is an indirect and possibly less reliable way to gather information, and requires an implicit assumption about the impetus of that given behavior. Yet, it is relatively less costly as it does not require the observer to investigate the situation directly and incur additional risk. For example, information about the quality of a patch may be obtained by observing the success of others within that patch (Doligez et al. 2002).

The goals of this study are (1) to determine if and how members of a small flock of birds transfer information about risk among themselves and (2) to determine how this transfer (or lack thereof) affects foraging and movement decisions both of the individual birds and the flock as whole. We address these questions using house finches (*Carpodacus mexicanus*) as a model species because they are abundant in our study area, are a relatively common prey species for *Accipiter* hawks (Roth et al. 2006), typically flock during the winter, and are amenable to living in captivity (e.g. Fernandez-Juricic et al. 2006). Overall, we found some evidence of limited information transfer about risk in these finches. However, movement between patches seemed to be based on an apparent majority rule complicated by dominance interactions.

Methods

House finches were studied in captivity during the winter of 2005–2006 in Terre Haute, Indiana, USA. We captured all finches at feeders baited with oil sunflower seed using hardware cloth box traps. We attempted to catch experimental subjects in the same flock during the same trapping attempt to help ensure that members of the experimental groups were at least somewhat familiar with one another. Upon capture, birds were held in cloth bags and transferred immediately to our enclosures. All birds were individually marked with a series of dots of white paint for identification purposes and then released into the enclosure.

Experimental Enclosures

Two enclosures were housed in an unheated warehouse approx. 25 m × 15 m in size. Each enclosure consisted of two patches (3.1 m × 3.1 m and 2.5 m tall) connected by 25 m of corridor (Fig. 1). The patches were arranged so that one observer could monitor both patches simultaneously. Birds in one patch could not see the other patch, although they could hear vocalizations from there. The observer sat in a blind behind windows made of one-way glass.

The enclosures were constructed of standard lumber with walls covered in Johns Manville Prowrap, a vapor barrier used in the manufacture of houses. This material was translucent, yet light, strong, and breathable. The floors and ceilings were covered in thick translucent plastic which (in the ceiling) readily transmitted light from overhead lamps, but prevented birds from seeing out of the enclosures. At no point during their captivity did the birds have visual contact with any outside objects or an experimenter.

Each patch contained a refuge made of a dense cluster of leafless vegetation (bush honeysuckle, *Lonicera maackii*, approx. 2 m tall, 1.5 m diameter) and *ad libitum* water and food. Food was provided in a feeder consisting of a ledge placed 10 cm off the ground and against the enclosure wall (Fig. 1a). A 3 cm × 7 cm hole was cut into the enclosure wall where it intersected the ledge, and food was placed just inside this hole. An opaque box was placed around the area outside of the enclosure around the feeder hole to prevent birds from escaping; additionally, the darkness created by the box dissuaded birds from passing through the feeder hole. The feeder hole allowed only one bird to feed at a time and required that the bird place its head into the hole to obtain food. The attack simulators, which consisted of life-sized model sharp-shinned hawks (*Accipiter striatus*) on a gravity-fed pendulum system controlled with a pulley, were built into the opaque box (Fig. 1b). The model hawks would swing down from the darkness of the opaque box in a high-speed approach toward any bird foraging through the feeding hole. The attacks were controlled remotely by the observer in the blind and could occur independently in both patches. We used lubricants on the pendulum and pull lines to ensure a silent attack; non-targeted finches showed no response to the falling pendulum itself during trials. With this design, only a bird that was actually feeding could see the

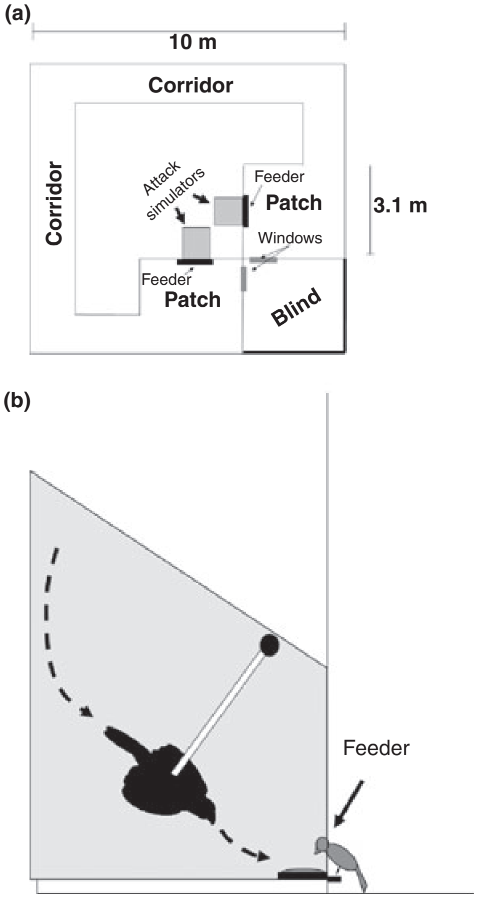

Fig. 1: Schematic diagrams of the (a) experimental enclosure and (b) attack simulator apparatus. (a) Two patches containing cover, water, and feeders were connected by approx. 25 m of corridor. The patches were arranged so that a single observer could view both patches simultaneously from a blind. (b) An attack simulator sat directly behind each feeder. A model hawk mounted on a pendulum was controlled by the observer and was launched for 'attack' when the appropriate bird placed its head in the feeder. Attacks could be observed by a bird only when it placed its head into the feeder; thus, individual attack sequence could be controlled. See text for details.

model hawk approach. As only one bird could feed at a time, we were able to control which bird observed a given predator attack.

Experimental Design

The experiment was arranged into a 4 d protocol. On day 1, three finches were captured and introduced into the enclosures in the morning. We included at least one member of each sex in all flocks, and over the course of the study, the ratio of males to females was approximately even. On day 2, birds were allowed to acclimate and the dominance hierarchy was determined by observation of aggressive behaviors. During days 1 and 2, we utilized training perches located throughout the corridor to ensure that birds were comfortably moving between patches. These perches were visible from the patches and illuminated to stimulate movement. At the end of day 2, the training perches were removed from outside of the enclosure and we verified that each flock had moved between the patches at least once. On day 3, the overall patch preference of the flock was determined as the patch in which the flock spent most of its time during a 3 h observation period. During this period, baseline data were collected on the frequency of patch switching as well as the feeding rate patterns of each bird. On day 4, apparent risk was increased in the preferred patch (now termed the ‘attack patch’) with simulated attacks. The previously non-preferred patch then became the ‘safe patch’, where birds were allowed to feed freely without attack. After the experiment, birds were banded and released at their capture site.

Attacks in the attack patch occurred over a 3 h period timed to correspond with the early-morning feeding bouts observed in the wild. The primary focal bird was attacked during the first hour during every attempt to feed that it made in the attack patch; the other two birds were allowed to feed undisturbed. During the second hour, both the primary bird and a secondary focal bird were attacked, while the tertiary bird was able to feed undisturbed. During the third hour, all three birds were attacked during every feeding attempt in the attack patch. In the vast majority of cases, the targeted birds were not able to acquire food while being attacked. Thus, the number of attacks also represents the number of times that an attacked bird returned to the feeder in an attempt to feed. To examine the effects of dominance in group decision making, we varied the placement of birds in the attack order according to dominance status. In one half of the trials (or groups), the dominant bird was the primary bird and the most subordinate bird was tertiary; in the rest of the trials, this order was reversed.

To determine whether finches transfer information about risk, we observed the feeding behavior of each individual in the group as different members of the group received attacks as described above. We determined the number of attacks incurred by each bird over time and the number of returns to the feeder after an attack. In addition, we also calculated the average latency (time in minutes) for each bird to return after it or any other bird left the feeder, either as a result of an attack or not. Latency observations greater than 15 min were removed because these lulls in feeding were likely to represent satiation rather than fear responses (T.C. Roth and S. L. Lima, personal observation). If birds were directly transmitting information about predation risk to each other, then we would expect all birds to greatly reduce their use of the feeder following an attack on any of the birds. Additionally, the time to return to the feeder should be on average greater after observing a flock-mate respond to a simulated attack vs. an observation after an undisturbed feeding bout.

To better understand the consequences of information transfer for group movement decisions, we examined the events leading to the group’s switch from the attack patch to the safe patch. We defined the group switch as the point in time at which the proportion of time spent in the attack patch dropped below the proportion of time spent in the safe patch. We ignored switch times within 5 min of the start or the end of the trial. To determine how the group decided to switch patches, we observed the time required to switch and the number of attacks on each bird before the switch occurred. If the group’s decision were made, for example, by the dominant individual and there were no information transfer, then we would have expected the group switch to occur shortly after the dominant bird was first attacked, regardless of whether that attack occurred during the first or last hour of the trial.

We used the data collected on day 3 as our baseline observation for each bird. For the feeding behavior analyses, we calculated the difference in number of feeding bouts during attacks from baseline and compared this difference value by time, dominance status, and dominance treatment. For the latency analyses, we used the baseline average latency for each bird as a covariate to determine if the latencies between feeding attempts depended on if the prior bird was attacked. Data were analyzed using general linear models in the statistical package

SYSTAT. Each bird was included three times in the models (once for each hour of observation). We used bird identity and baseline values as covariates to control for these repeated observations. Data were transformed to meet the assumption of normality when necessary. When data could not be transformed to meet these assumptions, non-parametric analyses were used.

Results and Discussion

Do Birds Transfer Information About Risk?

We found limited evidence for information transfer among individuals. We performed this experiment on 28 groups of finches (three individuals in each group; 14 groups in each dominance treatment) for a total of 84 individual finches. In all cases, repeated attacks on informed individuals did not dissuade naïve birds from feeding (Fig. 2). For example, during the first hour of attacks, when only the primary bird was being attacked, the secondary and tertiary birds continued to feed normally or even increased their feeding (Fig. 2). Not until all three birds were attacked during the third hour did all birds reduce feeding in the attack patch. For birds that had not yet experienced attacks directly, the level of feeding during the simulated attack day was not significantly different from baseline observations ($t_{83} = 1.134$, $p = 0.260$). In addition, with individual and time included as covariates, there was no significant effect of dominance treatment ($F_{1,164} = 0.056$, $p = 0.952$) or individual dominance status ($F_{1,164} = 0.167$, $p = 0.918$) on the difference in feeding from baseline (Table 1). When birds were attacked, they typically flushed to cover, but rarely gave vocalizations. These results suggest that our simulated attacks were perceived as risky (or at least disturbing) by the informed (attacked) birds, but do not suggest information transfer in that other birds did not reduce their feeding as we would have expected if the attacked birds were informing others of this risk.

However, in the case of the latency between feeding attempts, there was some evidence of information transfer. The time required for birds to return to the feeder after observing another bird's attack was significantly greater (11% higher on average) than that required when they observed their flock-mates leaving the feeder undisturbed ($F_{1,144} = 1.315$, $p = 0.033$; Table 2). There was no effect of dominance status or attack order in this analysis (Table 2). This result suggests that there was to some degree information about risk transferred to the naïve birds, perhaps in the form of an unusually abrupt departure from a feeder (e.g. Lima 1995b). However, the overall quality of the information transferred appeared to be low, as naïve birds were hardly dissuaded from frequent feeding.

Interestingly, informed birds that had been attacked continued to try to feed (and were

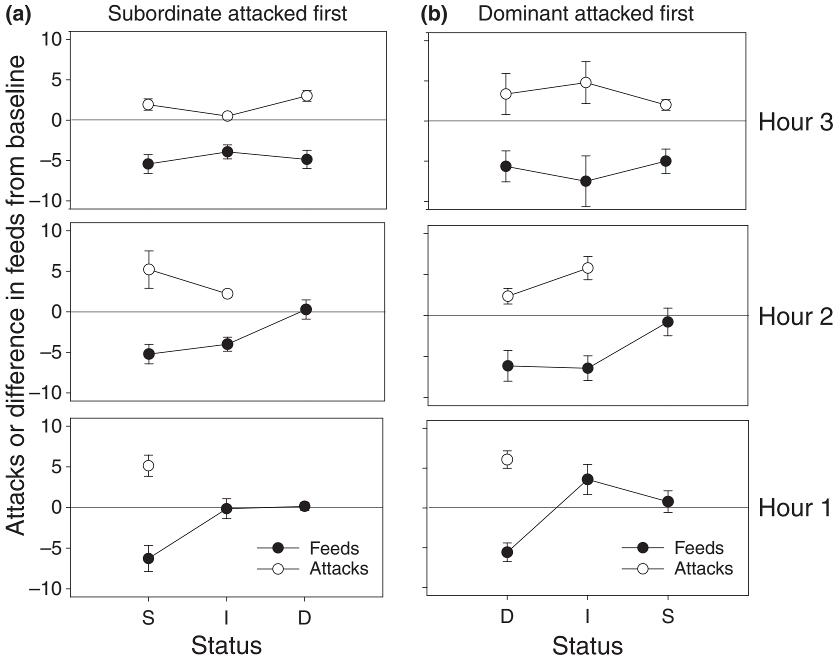

Fig. 2: Difference in the number of feeds from baseline (closed circle) and attacks (open circle) observed according to dominance status when the (a) subordinate and (b) dominant birds were attacked first over the course of the 3 h experiment. D = dominant, I = intermediate, and S = subordinate. Error bars = 1 SE.

Table 1: Analysis of variance of feeding behavior by dominance status (dominant, intermediate, subordinate) and treatment (dominant or subordinate attacked first) controlling for individual and hour of experiment

	SS	df	MS	F	p
Dominance status	0.17	1	0.17	0.01	0.92
Treatment	0.06	1	0.06	<0.01	0.95
Individual	4499.17	80	56.24	3.63	<0.001
Hour	494.53	2	247.27	15.95	<0.001
Error	2542.14	164	15.50		

Table 2: Analysis of variance of latency to return to feeder after observing another bird's attack-driven or unprovoked departure (departure type) by dominance status (dominant, intermediate, subordinate) and treatment (dominant or subordinate attacked first) while controlling for the individual's level of feeding during the baseline observation period

	SS	df	MS	F	p
Dominance status	0.26	2	0.13	0.47	0.628
Treatment	0.52	1	0.52	1.83	0.179
Departure type	1.32	1	1.32	4.65	0.033
Baseline	1.33	1	1.33	4.70	0.032
Error	40.69	144	0.28		

subsequently attacked again, Fig. 2), but often only after they observed naïve birds feeding. This may be the result of risk-informed birds relying more on public information about risk than on personal information. When one bird observes another individual foraging without being attacked, it can reasonably assume (in the real world, at least) that it is relatively safe to feed. *Accipiter* hawks only rarely return immediately after an attack to initiate another attack (Roth & Lima 2003; Roth et al. 2006). Thus, if one bird is attacked but subsequently observes others feeding safely, it may reasonably conclude that the hawk has left the area. Informed individuals thus seemed to be regularly updating their risk assessment using information derived from others' feeding behavior.

What are the Consequences of Information Transfer for Switching Patches?

In many cases, an individual wintering bird might do better not to split away from a flock. Leaving a flock might decrease the bird's chances of finding new foraging patches and reduce its likelihood of detecting a predator (Krause & Ruxton 2002). Furthermore, the isolated bird might need to increase its vigilance, which might lead to a reduction in foraging rate and an increase in its probability of starvation (Beauchamp & Fernandez-Juricic 2005). Thus, the movement behavior of the flock as a whole could be some sort of compromise among each individual's preferences and its unwillingness to leave the flock. Consequently, the aggregate behavior of flocks should be sensitive to the information possessed by each of its constituents. In our experiment, in addition to avoiding a feeder within a patch and the simulated predator attacks associated with it, the birds were able to avoid 'predation' by switching patches. Thus, we used the spatial behavior of the flock as a whole to further explore the influence of information asymmetries within the flock.

The mechanism behind a groups' switch to the safe patch seemed to be based on 'majority rule', but was complicated somewhat by dominance interactions. Of 28 groups, members of only third group did not move between patches during our observation periods; these groups, however, were known to move between patches during the training period. Individuals in the 25 groups that did switch patches at some point during baseline observations showed on average 65% more movement between patches during the attack treatment (Wilcoxon Z = 2.81, p = 0.005), suggesting that flock members perceived our attacks as disturbing and responded by moving to the other patch. Pooling across treatments, flocks tended to switch to safer patches once a majority (two out of three) of the birds had experienced attacks. However, a more complicated pattern emerged when the dominance status of attacked birds was taken into account. When the dominant bird was attacked first, groups generally switched after the second bird or third bird was attacked (i.e. during hour 2 or 3; Fig. 3). However, when the subordinate bird was attacked first, the group switched

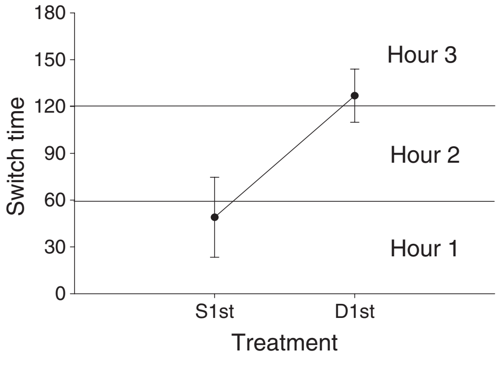

Fig. 3: Time at which the group switched from the attack patch to the safe patch when the subordinate (S1st) and dominant (D1st) birds were attacked first. Error bars = 1 SE.

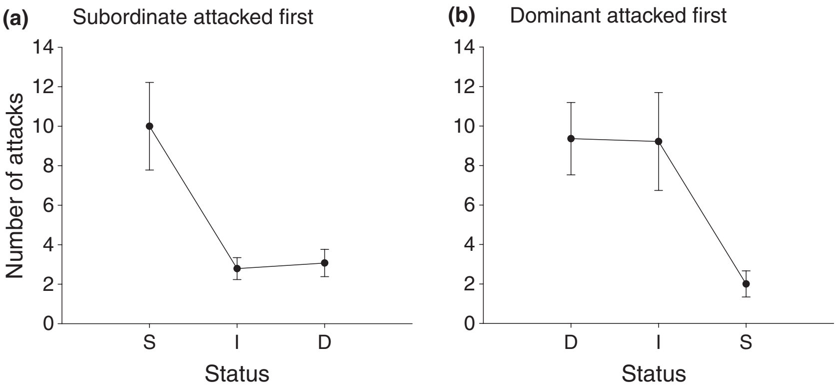

Fig. 4: Total number of attacks received before the group switch by dominance status when the (a) subordinate and (b) dominant birds were attacked first. D = dominant, I = intermediate, and S = subordinate. Error bars = 1 SE.

on average during the first hour (significantly sooner than during the dominant-first treatment, Mann–Whitney U = 35.0, $p = 0.028$; Fig. 3), and on average before a majority of birds were attacked. So, the 'majority rule' phenomenon might only occur when the subordinate bird is unaware of the potential risk.

When considering the number of attacks incurred by each bird, one can also see the consequences of patch switching times for individuals (Fig. 4). When the subordinate bird was informed, it received on average 10 attacks, while the other two received < 3 attacks each, a result of the early switch (Fig. 4a). When the dominant bird was informed, both it and the intermediate received around 10 attacks on average, while the subordinate bird received on average < 2 (Fig. 4b). We observed no effect of treatment ($F_{1,78} = 1.419$, $p = 0.237$) or status ($F_{2,78} = 0.012$, $p = 0.988$), but a strongly significant interaction ($F_{2,247} = 13.160$, $p < 0.001$) of treatment and status. Thus, the subordinate bird seemed to be the key in the dominance effect on group movement.

Overall, it appears that the subordinate bird may have been acting as a 'spatial anchor'. When the subordinate was informed of the risk in the patch, it tended to switch earlier to the other, safer patch, and the more dominant birds tended to follow (possibly to maintain the advantage of their dominance status or to maintain flock size). The end result seemed to be information transfer as naïve individuals (dominant and intermediate birds) followed the informed (subordinate) individual, but other observations suggest that no significant transfer of information can be inferred. For instance, when the subordinate bird was naïve and therefore had no incentive to switch patches, the dominant bird tended to stay in the patch and to receive additional attacks. The dominant individuals may have remained in order to maintain dominance or to guard the feeder. This latter explanation is supported by our observation that many of the additional attacks on the dominant bird occurred after it displaced the feeding subordinate from the feeder and subsequently attempted to feed itself. Thus, the reverse of the subordinate-first situation occurred. The dominant bird stayed in the patch and not until the intermediate bird was informed did the 'majority rule' and the switch occur.

The tendency of the subordinate bird to spatially anchor its flock likely results from its experiencing a different set of costs and benefits for staying in the group. In the absence of attacks, subordinates were often prevented from feeding by more dominant birds. However, when more dominant birds were startled from feeders by the simulated attacks, subordinate birds had greater opportunity to feed. Thus, the reaction of dominant birds to attacks actually increased the value of the attack patch to the subordinate bird. Consequently, the subordinate bird was likely reticent to leave the attack patch. The reluctance of the subordinate to leave the attack patch could in turn have anchored the entire flock to that patch because the other birds were also reluctant to split the flock by leaving.

Why is there relatively little evidence for information transfer in our finches? One reason could be that the members of the flock in this case are not a family group or will not remain in close proximity for any extended period. Thus, the diffusion of responsibility (*sensu* Taylor et al. 1990) relationships that might occur in such stable groups are not as likely and hence there is no long-term benefit of incurring personal costs to communicate information about risk. It is possible that the cues necessary for the direct transfer of information were obscured by the feeder apparatus. However, this is unlikely as only the head of the attack bird would have been briefly obscured. It is also possible that the short distance between cover and the feeder as constrained by our enclosure could have reduced the likelihood of direct information transfer, but alarm calls or other signals could easily have continued in the cover. Another possibility is that in a natural setting, relying principally on public information about risk may be a good tactic. When a single individual leaves the feeder while others remain, the likelihood of a predator encounter is probably low as others should also have seen the predator. If, however, multiple individuals simultaneously leave the feeder, then there might be more cause for concern (see also Lima 1995b). Also as mentioned above, hawks do not usually repeatedly attack a single area, but instead typically leave the area quickly after an attack. Thus, after an attack, short periods in cover should be sufficient and undisturbed feeding by others is likely a reliable signal that the predator is gone (e.g. DeLaet 1985; Hegner 1985). While public information may be useful in this situation, it may not always be the case in other situations or in other systems.

Future work on this topic should focus on the specific trade-offs involved in transferring information and in maintaining dominance. Dominant individuals may broadcast or assess information differently than subordinates, making information itself more valuable for some than for others. In addition, we need to consider other species with different levels of group relatedness and cohesion. While house finches are fairly social birds, other species with more stable social groups (e.g. parids) may show different levels of information transfer. For such species, we might expect more information transfer, as there is more benefit for reciprocity. In addition, the manner in which shared information is utilized may also vary with social structure.

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