

# Predator detection and avoidance by starlings under differing scenarios of predation risk

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Practically all animals must find food while avoiding predators. An individual's perception of predation risk may depend on many factors, such as distance to refuge and group size, but it is unclear whether individuals respond to different factors in a similar manner. We tested whether flocks of foraging starlings responded in the same way to an increased perception of predation risk by assessing three factors: (1) neighbor distances, (2) habitat obstruction, and (3) recent exposure to a predator. We found that in all three scenarios of increased risk, starlings reduced their interscan intervals (food-searching bouts), which increased the frequency of their vigilance periods. We then examined how one of these factors, habitat obstruction, affected escape speed by simulating an attack with a model predator. Starlings were slower to respond in visually obstructed habitats (long grass swards) and slower when they had their head down in obstructed habitats than when they had their head down in open habitats. In addition, reaction times were quicker when starlings could employ their peripheral fields of vision. Our results demonstrate that different sources of increased risk can generate similar behavioral responses within a species. The degree of visibility in the physical and social environment affects both the actual and perceived risk of predation. *Key words*: interscan interval, predation risk, starlings, vigilance, visibility, vision. [*Behav Ecol* 17:303–309 (2006)]

Predation risk can affect foraging patch selection, irrespective of the success of predators in catching prey (Lima, 1998). Animals use a number of behavioral strategies to enhance the probability of predator detection, such as flocking (Pulliam, 1973; Roberts, 1996) and adapting their search-scan behavior to their environment (Lima, 1992; Lima and Bednekoff, 1999; Whittingham et al., 2004). Rapid predator detection is crucial for animals that take evasive action to avoid capture, and this information can be obtained directly through detecting the predator (personal information) or indirectly through the detection of companions (social information, Danchin et al., 2004). For species that rely on detecting predators by sight, the risk of predation may be a function of visibility of the surroundings (Lima and Dill, 1990; Lima and Zollner, 1996), which is expected to affect the ability of animals to obtain not only personal but also social information. An understanding of how the degree of visibility affects the levels of predation risk is important in order to predict how changes in habitat structure affect patch quality and hence the distribution of individuals at local and regional scales (Butler et al., 2005; Lima, 1998; Whittingham and Evans, 2004).

In this paper, we are primarily concerned with exploring the effect of limited visibility on predator detection through personal and social scanning. Limited visibility effects can potentially reduce predator detection in at least two ways: first, an individual is less likely to spot the predator itself (Arenz and Leger, 1997; Whittingham et al., 2004), and second, an

individual takes longer to react to flock neighbors that spotted the predator earlier (Cresswell et al., 2000; Hilton et al., 1999). Limited visibility effects can be triggered by two factors, physical visual obstruction (vegetation blocking the visual field) and distance effects (information transfer decreases with distance from the source of information).

Information on the presence of predators is increasingly difficult to obtain as distance between flock members increases (Fernández-Juricic et al., 2004b; Lima and Zollner, 1996; Rolando, 2001) and as visibility decreases (Fernández-Juricic et al., 2005; Metcalfe, 1984). In visually obstructed environments, information about predators may be hidden behind obstructions, increasing perceived or actual predation risk (Arenz and Leger, 1997). Individuals that are spaced further apart may be under greater predation risk because they can be targeted by predators more easily (Quinn and Cresswell, 2004), and they have more difficulty spotting conspecifics reacting to predators (Hilton et al., 1999).

Our goal was to assess the behavioral mechanisms related to food searching and predator detection in scenarios with different levels of risk created through variations in visibility. We chose European starlings (*Sturnus vulgaris*) due to their known ability to use personal and social information to detect predators (Powell, 1974). The effects of visibility on starling scanning behavior were studied before (Fernández-Juricic et al., 2005) but only using artificial barriers that restricted visibility toward companions within the flock and not in other directions. Here we used foraging scenarios with obstruction manipulations that mimicked natural situations (grass mown to different heights), which would enhance the applicability of our results to the ecology of grassland species like the starling. We conducted the experiment using a repeated measures design with enclosures placed on natural foraging grounds under differing scenarios of risk. This allowed us to measure relative differences in behavior within individuals

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that we can attribute to changes in risk across our conditions. Seminatural experiments with enclosures are an accepted method in behavioral ecology to assess the foraging and vigilance responses of test subjects to manipulations (Butler et al., 2005; Cresswell et al., 2003; Powell, 1974; Tinbergen, 1981) because the behavior of animals is generally similar to that exhibited in natural situations (Fernández-Juricic et al., 2005; Olsson et al., 2002; Whitehead et al., 1995).

Animals that rely on vision are at greatest risk of being predated when they are not vigilant but are performing some other task such as foraging or sleeping because they cannot detect and escape from predators. Models of antipredator vigilance predict that animals under higher predation risk should decrease the nonvigilant period, the interscan interval (Bednekoff and Lima, 1998; Scannell et al., 2001), which for a foraging bird is the food-searching period. We hypothesized that starlings would respond to different scenarios of increased predation risk in a similar manner by shortening their head-down periods and increasing their frequency of scanning. We then answered four questions by conducting two experiments. (1) How do starlings alter their foraging and scanning strategies when further apart? (2) How do starlings alter their foraging and scanning strategies in response to habitats with different grass height? (3) How do starlings alter their foraging and scanning strategies after exposure to a model hawk? (4) How is predator detection affected by limited visibility? In experiment 1, we manipulated grass height and neighbor distance and assessed the foraging and scanning behavior of starlings. In experiment 2, we manipulated grass height and the presence of a predator and compared foraging and scanning behavior before and after animals were exposed to an attack and also determined predator detection speeds. If starlings respond to reduced risk by increasing their nonvigilant foraging periods, we expected to see an increase in food intake when visibility was increased (e.g., on short swards and when neighbors were close). Increased intake could also occur because prey are more accessible on short swards as they are easier to spot and less obstructed by vegetation. If this is true, we expected intake rates (prey captured per second of foraging) to be greater on short swards than taller swards, whereas if the benefit of foraging on short swards is due to a reduction in predation risk (by scanning while foraging), we expected longer foraging periods on short grass but no difference in intake rates.

## METHODS

We conducted two experiments to answer our four questions. For both experiments, starlings were captured at University Farm, Wytham, Oxfordshire, under English Nature license. They were housed in groups of two and three in  $0.9 \times 0.7 \times 0.6$ -m indoor enclosures under a light:dark cycle that reflected prevailing conditions and were in visual and auditory contact with other groups. They received a diet of turkey starter crumb, Orlux softbill pellets, and mealworms (*Tenebrio monitor*). Water was available ad libitum. In experiment 1, animals were not food deprived, but their food bowls were not replenished until the trials were finished. In experiment 2, animals were food deprived for 2 h before their trial.

Experiment 1 (corresponding to questions 1 and 2) was carried out between January and March 2002 using 25 adult starlings. We used a  $2 \times 2$  factorial experimental design to investigate the effects of (1) variations in nearest neighbor distances (0 and 5.5 m) and (2) habitat visibility (short 3-cm grass and long 13-cm grass). Treatments were randomly allocated to each of eight blocks in a permanent pasture field to minimize any effects of natural variation in prey abundance, primarily leatherjackets (Tipulidae) (Dunnet, 1955, 1956),

and predation risk. Four bottomless  $0.5\text{-m}^3$  cubic mesh enclosures were arranged in a square within a block with either their sides touching (0-m neighbor distance) or with 5.5 m between enclosures. Mowing frequency was the same in both treatments, and blocks were covered with netting to prevent depredation from wildlife and were used only once. Trials were not performed during rain, strong wind (Beaufort force  $> 4$ ), or when the ground was frozen or covered by frost.

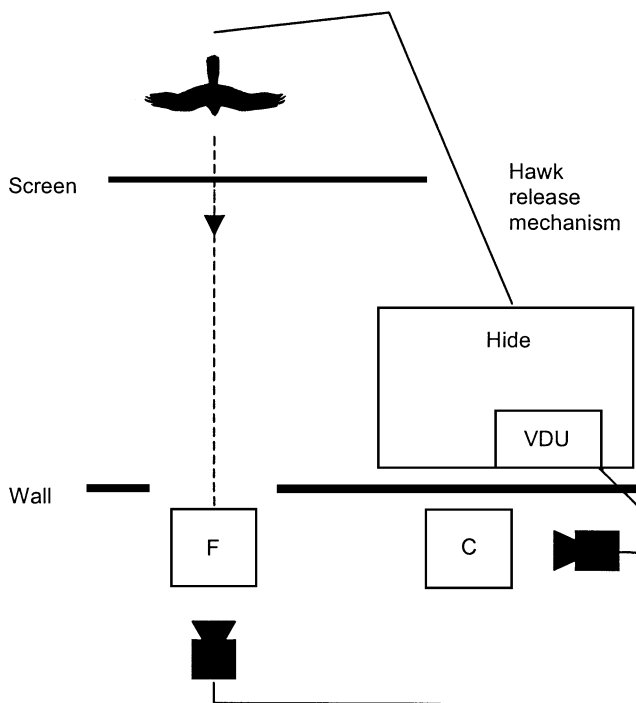
Twenty of the 25 starlings were randomly chosen as focal individuals (11 males and 9 females), and each focal had three companions selected from the remaining stock. Each focal bird had the same companions for all its treatments and served as a companion for two or three other focal birds. Four trials were performed each morning and neither the focal nor the companion birds received more than one foraging trial in a day. Birds were tested in groups of four consisting of one focal with its three companions each in individual enclosures. The behavior of the focal individual was recorded using a digital video camera placed 3 m away. A trial lasted 15 min after probing for prey commenced, which was usually about 1 min after release. Each focal individual received one replicate of each treatment, resulting in 80 trials (20 birds  $\times$  two levels of neighbor distance  $\times$  two levels of grass height). Birds were released at the capture site once all trials were completed.

Experiment 2 (corresponding to questions 3 and 4) was performed during November and December 2003 using 76 adult and juvenile starlings. It was designed to test the effects of predator exposure on foraging and scanning strategies and to quantify the effect of a predator attack in substrates with different visibility on the time taken to detect the predator. We did not manipulate neighbor distance due to spatial restrictions where the experiment was conducted. Each individual received one trial in either a high-visibility habitat (short 3-cm grass) or a low-visibility habitat (long 13-cm grass). Foraging and scanning behaviors were recorded both before and after a simulated hawk attack. A pilot experiment demonstrated that starlings sensitized to simulated hawk attacks, preventing us from using a repeated measures design. All individuals were released after a single exposure to the experimental treatment.

Experiment 2 was conducted inside a greenhouse that was divided into two rooms (Figure 1). Two  $0.5\text{-m}^3$  cubic mesh enclosures were placed in the lower room onto foraging trays on top of a 1-m-tall table. The left enclosure was assigned to the focal individual and was placed across the interconnecting doorway, and the companion enclosure was placed 1 m to its right. Each enclosure was on a turf square that covered the foraging tray, a plastic  $0.5\text{-m}^2$  tray containing a base of wet sand. The turf was a ryegrass (*Lolium perenne*) silage mix and was sown at a rate of  $50\text{ g m}^{-1}$  onto a 1-cm-deep layer of vermiculite, an inert growing media. The developing sward formed a root mat around the vermiculite that enabled it to be lifted, cut into  $0.5 \times 0.5\text{ m}^2$ , and placed onto the foraging tray, at which time it was trimmed to either 3- or 13-cm height. Starlings can easily probe through such turfs and extract mealworms hidden beneath (Devereux CL, personal observation).

A taxidermic model of a juvenile female sparrow hawk *Accipiter nisus* mounted in flight position was suspended from a wire at the apex of the top greenhouse room. The wire ran to the base of the table on which the focal enclosure was placed, 10 m away (Figure 1). To simulate an attack, the hawk was flown down the wire, approaching the focal enclosure at speeds of approximately  $13.5\text{ km h}^{-1}$ . A screen hid the hawk until it reached the midpoint, and after reaching the focal enclosure it disappeared from sight under the table.

Food was removed from holding enclosures for 2 h prior to trials. For each trial, 50 live mealworms were placed on top of



**Figure 1**  
Experimental set up. Two starlings, the focal (F) and companion (C) were allowed to forage for buried mealworms on grass turfs in individual enclosures. The hawk was released by the experimenter sitting in the hide by pulling the release mechanism. The hawk flew down a wire toward the focal bird and appeared once it passed a screen. The subject's behavior was monitored on a VDU by the experimenter and recorded on two video cameras placed behind the focal bird and to the side of the companion bird. Figure not to scale.

the wet sand in each foraging tray and covered with a fresh turf square. One bird was placed in each enclosure (thereafter called the focal and companion birds), and their behavior was recorded using a digital video camera positioned behind the focal enclosure and to the side of the companion enclosure (Figure 1). The focal bird was either an adult or a juvenile, and the companion was an adult of the same sex. The companion bird could see the focal bird but could not see the hawk, and the focal bird could see both the companion and the approaching hawk. White noise was played through two speakers during the trial to reduce external disturbance. The trial was observed remotely on a video monitor. Once both birds had foraged for at least 2 min, and while both were actively foraging, the hawk was released. The simulated attack caused an escape reaction in both birds. After the attack, the birds were left to settle and recommence foraging, which was usually within 2 min, and the trial continued either until both birds had foraged for more than a minute or until 10 min had elapsed without foraging by one or both birds.

Behavioral data was extracted from videotapes using Noldus Observer Video Pro 4 (Noldus Information Technology, 1997). Two states with measured duration (head up, head down) and three instantaneous events (probe, root, eat) were recorded. We distinguished between time spent actively foraging and time spent performing other behaviors, and results are restricted to the periods of active foraging. An active foraging bout was initiated with a head down (head below the body's horizontal plane) and terminated by a head up (head above the body's horizontal plane) lasting longer than 5.6 s, the median duration recorded from the first experiment for

this behavior. Probe and root were both prey-searching behaviors occurring during head downs. Probe was classified as the initial investigation that caused a hole in the substrate, and a root was a further stab within the hole that functions to expand it. All active foraging bouts were analyzed for each 15-min trial in experiment 1 (questions 1 and 2).

To determine the effect of predator exposure on foraging and vigilance variables in experiment 2 (question 3), we selected a snapshot of each bird's foraging behavior, which was the sum of complete active foraging bouts either pre- or post-attack until they equaled or exceeded 10 s of foraging, excluding nonforaging behaviors.

For questions 1–3, the following behavioral response variables were computed from videos: mean duration of a searching bout (s), search rate (number of head downs performed per second of foraging), mean duration of a scan (head up), scan rate (number of head ups per second of foraging), probe rate (probes per second of foraging), root rate (roots per second of foraging), and intake rate (prey per second of foraging). Intake rate was not possible to compute for question 3 because of the shorter time frame.

We used factor analysis on the starling's behavioral responses using the principal component (PC) extraction method to reduce the multidimensionality of our data set. The resulting factors (i.e., PCs) are composite and uncorrelated variables that summarize the variation in foraging and vigilance behavior seen. We then used the scores of PCs as the response variables in repeated measures general linear models (GLMs) (all analyses were conducted in SPSS for Windows v 13.0.1, SPSS Inc., Chicago, Illinois, USA). For questions 1 and 2 (experiment 1), we constructed a full-interaction model with neighbor distance and grass height as two within-subject factors and sex as a between-subject factor. For question 3 (experiment 2), we used a full-interaction model with grass height, age, and sex as between-subject factors and before/after predator as a within-subject factor.

To evaluate question 4 (experiment 2), the videos of each attack were analyzed frame by frame to determine the reaction speed to the hawk. At the point at which the hawk first appeared to the bird, the following variables were recorded: head position (head up, head down) and orientation (facing toward hawk, side on to hawk, or facing away from hawk). The speed of the hawk when it was visible to the focal bird was computed from the time taken for it to travel a set distance along the wire. The latency to react was taken as the difference between the first appearance of the hawk and the first reaction of the focal bird, regardless of the type of reaction (e.g., crouch, fly, run). We analyzed this data using a GLM in Minitab Release 14.1 (Minitab Inc., State College, Pennsylvania, USA) and specified response time as the dependent variable and grass height, head position, head orientation, age, sex, body condition, and hawk speed as our independent variables.

## RESULTS

### Experiment 1

From the data set of experiment 1 (questions 1 and 2), two factors, which had eigenvalues  $>1$  and represented all the behavioral variables studied, were used. Factor 1, which explained 44.9% of the variance, represents the contrasting effect of search, scan, and probe rates, with search length (Table 1). High PC1 scores represented a strategy of frequent switching between scanning and short searches, with high probe rates. Factor 2, which explained a further 29.2% of the variance, represents the contrasting effect of root and intake rates, with scan length. High PC2 scores represented increased vigilance and a low foraging intensity (Table 1). There

**Table 1**  
Loadings of the seven foraging and vigilance variables on the first two principal component analysis axes from experiment 1

Variables	PC1	PC2
Eigenvalue	3.14	2.04
Percentage variation explained	44.9	29.2
Search length	-0.522	-0.139
Search rate	0.483	0.258
Scan length	-0.234	0.485
Scan rate	0.461	-0.211
Probe rate	0.473	-0.027
Root rate	0.001	-0.606
Intake rate	-0.052	-0.516

were no significant interactions between neighbor distance and grass height in GLM analyses on the response variables PC1 or PC2. There were no significant interactions between either neighbor distance or grass height and the between-subject factor, sex.

- (1) How do starlings alter their searching and scanning strategies when further apart?

Starlings foraging further apart had significantly higher PC1 scores ( $F_{1,17} = 14.51$ ,  $p = .001$ ) translating into a strategy of short searches and scans. We did not detect a significant relationship between neighbor distance and PC2 scores ( $F_{1,17} = 1.22$ ,  $p = .285$ , Power = 0.18).

- (2) How do starlings alter their search and scan strategies in response to limited visibility?

Starlings foraging in reduced visibility habitats (long grass) had higher PC1 scores ( $F_{1,17} = 4.75$ ,  $p < .05$ ) and lower PC2 scores ( $F_{1,17} = 6.22$ ,  $p < .05$ ). In short grass habitats with improved visibility, starlings foraged for longer periods and searched patches more intensely, as reflected by a greater root rate, and consequently had a greater intake rate.

## Experiment 2

From the data set of experiment 2 (question 3), two factors were extracted that had eigenvalues  $>1$  and represented all the variables studied. PC1 explained 46.4% of the variance and had high positive loadings for search length and high negative loadings for search, scan, and probe rates (Table 2). Low PC1 scores represented a strategy of frequent switching between scanning and short searches, with high probe rates. PC2 explained a further 30.7% of the variance and had a high positive loading for scan length and a high negative loading for root rate (Table 2). High PC2 scores represented increased vigilance and a low foraging intensity. There

**Table 2**  
Loadings of the six foraging and vigilance variables on the first two principal component analysis axes from experiment 2

Variables	PC1	PC2
Eigenvalue	2.79	1.84
Percentage variation explained	46.4	30.7
Search length	0.445	-0.332
Search rate	-0.750	-0.095
Scan length	0.227	0.633
Scan rate	-0.518	-0.224
Probe rate	-0.366	0.188
Root rate	0.155	-0.628

were no significant first-order interactions between the within-subject factor and any of the between-subject factors.

- (3) How do starlings alter their foraging and scanning strategies after the appearance of a model hawk?

Following the appearance of the model hawk, starlings had significantly lower PC1 scores ( $F_{1,21} = 14.98$ ,  $p = .001$ ) and significantly higher PC2 scores ( $F_{1,21} = 18.02$ ,  $p < .001$ ). Starlings increased the length of their scans and reduced their search length and root rate, increasing scan rate, following the appearance of the hawk.

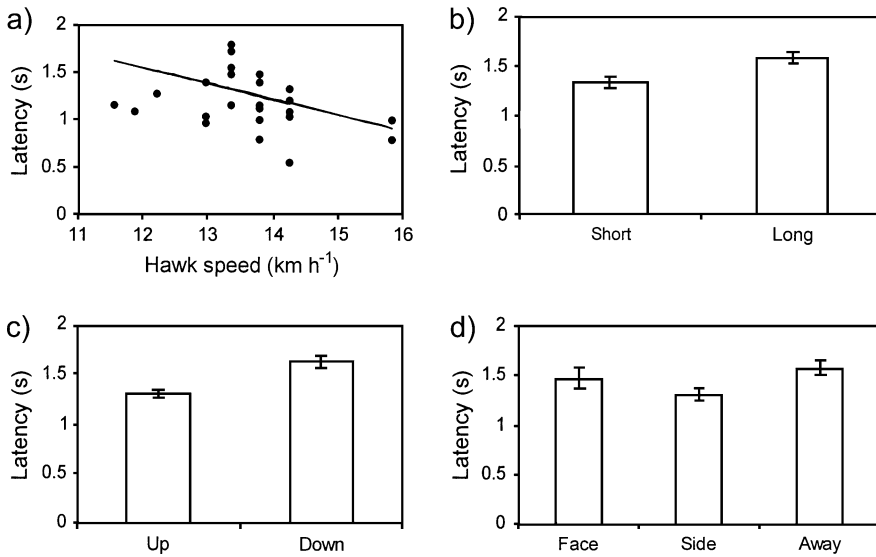
- (4) How does limited visibility affect predator detection?

Starlings foraging on long grass, a visually obstructed habitat, took longer to react to the simulated hawk attack than those foraging on short grass ( $F_{1,18} = 6.80$ ,  $p < .02$ , Figure 2). Other factors that influenced reaction speed were the speed of the approaching hawk ( $F_{1,18} = 10.22$ ,  $p < .01$ ), whether the starling was head up or head down ( $F_{1,18} = 17.48$ ,  $p = .001$ ), and the orientation of starling's head ( $F_{1,18} = 5.61$ ,  $p < .02$ ). Starlings were faster to respond when the hawk speed was greater, when they were head up rather than head down and when they were side on to the hawk compared to when they faced toward or away from the hawk (Figure 2). Explanatory variables that did not affect predator detection were age ( $F_{1,18} = 0.2$ ,  $p = .66$ ), sex ( $F_{1,18} = 0.00$ ,  $p = .95$ ), and body condition ( $F_{1,18} = 2.41$ ,  $p = .14$ ). The data set was split in two according to whether the subject was head up or head down at the point of attack, and each was analyzed independently for the effect of grass height on reaction time. There was no effect of grass height on the time taken to react to the hawk for starlings that had their head up when the hawk appeared ( $F_{1,13} = 1.54$ ,  $p = .24$ , Figure 3). However, when starlings had their head down, their reactions were 11% (0.16 s) quicker on short grass than they were on long grass ( $F_{1,5} = 9.05$ ,  $p = .03$ , Figure 3).

## DISCUSSION

Our results show that the mechanisms of scanning and food exploitation are adjusted to the perception of predation risk and that different sources of increasing risk generate similar behavioral responses. For instance, starlings decreased the duration of searching bouts (interscan intervals) but increased their rate when foraging further apart, when their field of view was obstructed in long grass and following the appearance of a predator. As a result, starlings decreased the rate of exploration within a given patch (root rate) and increased their scanning rates in all three scenarios of increased predation risk. Moreover, the chances of predator detection depend on environmental (grass height) and morphological (body and head postures) effects on visibility.

The effects of visibility on predation risk should be discussed in the light of the visual perception of starlings as it is the ease with which individuals gather information from the environment (e.g., predators, conspecifics) that affects foraging and scanning strategies (Fernández-Juricic et al., 2004a). Starlings have a visual system divided into three areas: binocular (specialized on food handling but with low visual depth), peripheral (specialized on detecting objects at far and close distances), and blind areas at the rear of their heads (Martin, 1986). The starling's retina is structured to allow both near and far objects to be focused simultaneously, and their peripheral visual fields are wide enough to scan the horizon and sky without lifting the head (Martin, 1986). Recent evidence shows that this visual field configuration allows starlings to gather visual information about conspecifics while



**Figure 2**  
The effects of (a) predator speed, (b) grass height (3 cm short and 13 cm long), (c) head position (up or down), and (d) head orientation (facing hawk, side on to hawk, away from hawk) on the latency to react to a model hawk attack. Bars represent means  $\pm$  SE.

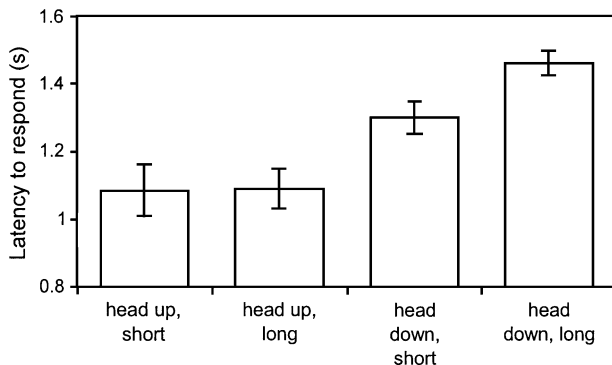
head down, although the quality of that information may be reduced (Fernández-Juricic et al., 2005). Dark-eyed juncos prefer to feed in open environments that permit peripheral vision and alter their vigilance behavior when head-down vigilance is obstructed (Bednekoff and Lima, 2005). Many social foraging models assume that vigilance and foraging are mutually exclusive behaviors (Pulliam et al., 1982; Scannell et al., 2001; Ward, 1985). This study adds to growing evidence that they are not so (Cresswell et al., 2003; Guillemain et al., 2001; Lima and Bednekoff, 1999).

Under our experimental conditions, we hypothesized that short swards would be better than long swards for foraging starlings, firstly because prey would be more readily available and/or secondly because vigilance could occur while feeding (Devereux et al., 2004; Fernández-Juricic et al., 2005). If prey were more available on short swards, we expected intake rate (prey captured per second of foraging) to be greater, whereas if short swards were more profitable because they allowed vigilance and foraging to occur simultaneously, we expected more time to be devoted to foraging, a lower scanning rate, and subsequently more prey to be captured overall without a change in intake rate. Our results suggest that both might be happening concurrently. Chaffinches *Fringilla coelebs* feeding on seeds in similar experimental conditions do not alter

search times between clear patches and those with a limited field of view (Whittingham et al., 2004). This is probably because they are constrained by their individual foraging ability: they are already searching for seeds in patches with a clear field of view as fast as possible. In addition, animals that can perform the bulk of their foraging task while the head is raised (e.g., dehusking seeds) can be overtly vigilant while simultaneously foraging without loss to the quality of vigilance information (Cowlshaw et al., 2004). The foraging task for insectivorous species, such as starlings, is very different from that of granivorous birds. Starlings probe the ground for food (Feare, 1984), and only around 4% of probes are successful (this study). In contrast, Whittingham et al. (2004) recorded chaffinches picking up seeds on 83% of searches. It therefore seems likely that starlings may be more willing to alter their head-down searching strategy to cope with increased risk.

Habitat complexity has been shown to influence vigilance patterns in some other birds, such as ducks (Guillemain et al., 2001), waders (Metcalf, 1984), and passerines (Lima and Bednekoff, 1999). In our visually obstructed patches, starlings compensated for not being able to scan while foraging by increasing their scan rate through shortening search bouts and consequently reducing prey intake. In addition to monitoring their environment for predators, starlings could scan other flock members to gather information relative to predation risk (Fernández-Juricic et al., 2004b; Powell, 1974). Shared predator vigilance could lower individual risk by increasing the chances of escape should an attack occur (Roberts, 1996). Increasing neighbor distance would reduce information flow, with a potential decrease in the benefits of group foraging. Scan rate was higher in long swards and when neighbors were more distant and lowest on short swards and when neighbors were very close. Analogously, red-billed choughs, *Pyrrhonorax pyrrhonorax*, which feed in a similar manner to starlings are more vigilant when their nearest neighbors are more than 3–6 m away (Rolando, 2001).

In high-risk scenarios (model predator attack), starlings showed similar behavioral responses to increasing risks than those reported for low-risk circumstances (no predator attack). The increase in scanning rate after the appearance of the predator has been reported before (e.g., Glück, 1987) as a strategy to increase the chances of detecting a predator that may resume an attack. Individual chaffinches that scanned more frequently when foraging responded more rapidly to



**Figure 3**  
Relationship between grass height (3 cm short and 13 cm long) and head position (up or down) on the time taken for a foraging starling to react to a model hawk attack. Bars represent means  $\pm$  SE.

a model predator (Cresswell et al., 2003) and their vigilance levels increased with habitat obstruction, but chaffinches were not able to fully compensate for reduced visibility in obstructed habitats as response times were slower (Whittingham et al., 2004). Our results show that limited visibility in tall sward patches also reduces detection time in starlings and that this response is affected by morphological limitations of their visual systems. Individuals in head-down posture when the hawk appeared had longer reaction times than in head-up postures, which underscores the lower quality of head-down scanning in this species (see also Fernández-Juricic et al., 2005). Studies in other species support a lower detection rate while head down (Lima and Bednekoff, 1999; Whittingham et al., 2004). Furthermore, the configuration of the visual fields while head up also affected detection. Similar results have been found in blue tits *Parus caeruleus*, which took longer to detect predators when their back was orientated toward a predator compared to when they were side on to it (Kaby and Lind, 2003). These novel results point out the importance of understanding the perceptual abilities of different species to predict risk sensitivity in different habitats (Fernández-Juricic et al., 2004a).

Our behavioral results also have applied implications. Over the past four decades, many species of birds inhabiting farmland across the UK and northwestern Europe have declined in abundance, which has been attributed to changes in agricultural practices (Donald et al., 2001; Krebs et al., 1999). Starling populations have declined more than 50% in the past 25 years in Britain, as have many northern European populations (Gregory et al., 2002, 2004; Robinson and Sutherland, 2002; Siriwardena et al., 1998). During the period of the UK decline, starling breeding performance has shown a slight but significant improvement, while survival of first years and adults has fallen, probably because of a reduction in food or habitat availability (Crick et al., 2002; Freeman et al., 2002; Siriwardena and Crick, 2002). Several studies have correlated habitat features, such as short vegetation in agricultural grassland, with the abundance of starlings and other insectivorous species (Barnett et al., 2004; Perkins et al., 2000; Tucker, 1992; Vickery et al., 2001). Often these features may be correlated with other aspects of the environment (e.g., land management), which may affect food abundance (see Chamberlain et al., 1999). Our results provide a mechanism, predation risk, to explain bird-habitat correlative studies, even in the absence of changes in food availability (e.g., Perkins et al., 2000; Whitehead et al., 1995).

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