ANIMAL BEHAVIOUR, 2007, **74**, 1381–1390
doi:10.1016/j.anbehav.2007.01.005

Changes in vigilance and foraging behaviour with light intensity and their effects on food intake and predator detection in house finches

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*(Received 3 May 2005; initial acceptance 15 July 2005;
final acceptance 23 January 2007; published online 1 October 2007; MS. number: A10148R2)*

Animals foraging in groups face different challenges, like avoiding predators and competing for food. One factor that has received little consideration is illuminance. Social animals exploiting sunlit patches could image the sun on their retinas, restraining visual perception, and, as a result, the use of personal and social information. Our goal was to assess the effects of illuminance under different levels of predation risk by studying pairwise interactions in house finches, *Carpodacus mexicanus*. We manipulated predation risk levels (low and high) and illuminance (low and high), and recorded changes in patch use, scanning and foraging behaviour, food intake rate, and predator detection. We found that illuminance affected the behaviour of house finches, which (a) avoided sunlit patches, (b) changed vigilance behaviour under high illuminance by reducing scan bout duration, (c) reduced foraging attempts under high light conditions, although food intake was not affected, and (d) increased the latency to detect a predator attack when foraging in pairs under high light conditions and when conspecifics showed antipredator responses that were more difficult to detect visually. If personal and social information sources about predation risk are restricted in sunlit patches, animals might increase their perceived predation risk. We discuss alternative interpretations, such as higher predation risk in sunlit patches due to greater visual exposure to predators. We suggest that heterogeneity in light conditions should be considered an ecological factor affecting foraging and antipredator behaviour in groups.

Keywords: antipredator behaviour; *Carpodacus mexicanus*; glare; house finch; illuminance; predator detection; predation risk; scanning; social information; vigilance

The perceptual environment of birds is highly visual because of their relatively large eyes in relation to their body sizes (Cook 2001). Visual environments are rich in information (shapes, colours, movements, etc.), but birds select the information available so that they can improve fitness-related parameters (Dukas 1998). For instance, animals engaged in a complex foraging task increase their visual attention towards distinguishing food items, but, as a result, decrease their ability to detect peripheral objects (Dukas & Kamil 2000). For social species, we can expect an even more diverse visual environment with greater information load (presence, identity, and behaviour of conspecifics; Danchin et al. 2004; Fernández-Juricic et al. 2004a). For example, animals can look out for predators themselves (personal information) or get that information from other flockmates (social information) (e.g. Hilton et al. 1999; Cresswell et al. 2001). The ability to gather social information would depend on a signal-to-noise ratio (Dall et al. 2005): when the visual costs of acquiring such information are too high, animals are expected to modify their behaviour to compensate for the lack of information or to resort to personal information (reviewed in Giraldeau et al. 2002; Valone & Templeton 2002). However, we still know relatively little about the fitness consequences of such behavioural decisions (but see Templeton & Giraldeau 1995; Kendal et al. 2004; Bednekoff & Lima 2005).

Visual information gathering is impaired under low light conditions (namely, from just before dawn until sunrise or

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0003–3472/07/$30.00/0

at night), which has been widely studied and implicated in the functional significance of the morning singing in birds (e.g. Kacelnik 1979; Hutchinson 2002; Thomas et al. 2002), and the variations in vigilance between moonless and moonlit nights (Beauchamp & McNeil 2003). However, as important, but less studied, is how patches with high illuminance affect visual information gathering. Animals in sunlit patches could image the sun on their retinas. Sunlight could act as a secondary source from which light is bounced around inside the eye chamber, restraining visual perception, which may lead to disability glare (Martin & Katzir, 2000). Birds with large eyes are more sensitive to imaging the sun because of their greater visual acuity, but have usually developed sun shading structures (e.g. enlarged brows, hair like feathers on the eye lids and around the eye) or large blind areas at the rear of their heads to minimize this effect (Martin & Katzir, 2000). However, birds with smaller eyes, which have narrow blind areas and lack sun shading structures, are likely to regularly face sun imaging problems when exploiting patches with varying illuminance, which could affect not only personal but also social information gathering, and eventually the costs and benefits of living in groups.

We studied how variability in illuminance affects antipredator behaviour. Specifically, we assessed the simultaneous role of two factors, predation risk levels (before and after a predator attack), and light conditions (sunny or shaded patches), in different behavioural responses (patch use, and scanning and foraging behaviour) and two fitness-related parameters: food intake rate as an indirect indicator of body condition, and predator detection time as an indirect indicator of survival to predation events. We evaluated the transmission of social information relative to a predator attack by assessing predator detection time under different light conditions in relation to the presence or absence of companions, and the type of companion response to the predator. Assessing these various responses can help us understand the different levels at which antipredator behaviour occurs (Lind & Cresswell 2005), as individuals usually face the exploitation of patches with different levels of predation risk (e.g. Cresswell & Whitfield 1994; Whitfield 2003) and illuminance (e.g. Thomas et al. 2004).

Our model species was the house finch, *Carpodacus mexicanus*, which joins groups during the nonbreeding season, but also shows relatively high degrees of aggressive interactions within groups (Brown & Brown 1988; Shedd 1990). We created a heterogeneous environment under seminatural conditions with a refuge patch connected to a foraging patch. We studied pairwise interactions, which could limit the generality of results because they may not scale up to what normally constitutes a flock. However, our experimental approach seemed more appropriate to assess antipredator behaviour in social contexts, because larger group sizes could generate synergistic effects on the transmission of social information (Fernández-Juricic & Kacelnik 2004) that could make interpretations more difficult.

We were particularly interested in how predation risk and illuminance would interact, possibly generating compensatory mechanisms; however, there is no theoretical body predicting the direction of this interaction. Thus, we generated simple predictions based on current knowledge. High light conditions are expected to decrease the signal-to-noise ratio when animals try to obtain personal or social information. This could be caused by animals avoiding imaging the sun, or by other mechanisms (see Discussion). We predicted that house finches would compensate for a reduction in the quality of information by changing their scanning behaviour: decreasing scan bout duration to avoid negative effects on the retina (Martin & Katzir, 2000), but increasing scanning rate to maintain a certain amount of information per unit time. However, this compensatory mechanism might not be enough to detect a predator swiftly; thus, we predicted that reaction times through personal or social information would increase with high illuminance. For instance, animals may detect different conspecific responses to predators quickly under low light conditions. However, high light conditions may limit the ability to distinguish between subtle (crouching) and overt (flushing) conspecific responses, which would delay predator detection time. Finally, we predicted that under low predation risk animals would reduce their intake rate with high illuminance because of increasing difficulty to detect food items as a result of higher reflection from the ground. However, the difference in food intake rate between light conditions would be reduced under high predation risk, because animals would devote most of their time to monitoring for predators.

METHODS

Study Site and Species

We conducted the study at California State University Long Beach (CSULB) campus from 1 August to 17 September 2004, in the mornings from 0800 to 1300 hours on a grassy area shaded by an old Italian stone pine, *Pinus pinea*. This area was 25 m away from the closest pathway, which received low pedestrian traffic, so noise levels were minimized. The area, often used as a foraging spot by wild house finches, was surrounded by a 1.80-m-high fence covered with black plastic to screen out all external visual stimuli. The foraging behaviour of house finches in our seminatural set-up was similar to that shown by individuals in natural conditions (E. Fernández-Juricic, personal observation).

We caught and colour-ringed 75 adult house finches belonging to two populations in southern California: Seal Beach and Bolsa Chica. Animals were housed in indoor cages (0.85 m × 0.60 m and 0.55 m high), under a 12:12 h light:dark cycle (lights on at 0800 hours) at Animal Facilities. Birds were in visual and auditory contact, with two to three birds per cage. Water and food (finch mix; Royal Feeds, Leach Grain and Milling, Co., Downey, California, U.S.A.) were available ad libitum except during experimental trials and the preceding periods of food-deprivation. Experimental protocols were approved by the IACUC at CSULB (Protocol no. 206).

While testing housing conditions before starting this study, we detected a certain level of mortality (35.71% of 14 individuals) after 48 h (most of the deaths were caused by head trauma due to contact with the cages). For ethical reasons, we changed our design by capturing an animal, testing it only once the next day, and releasing it before 48 h in the same location where it was captured. This strategy increased bird survival to 100%, and was eventually adopted for the present study (see also Whittingham et al. 2004). Consequently, each data point corresponded to a different individual.

Many mechanisms could be implicated in the responses of animals to group conditions (reviewed in Beauchamp 1998, 2003; Giraldeau & Caraco 2000; Krause & Ruxton 2002); however, we controlled for some of them by blocking physical, but not visual, interactions among birds to avoid kleptoparasitism, controlling food-deprivation levels to minimize changes in focal behaviour with hunger, and supplying relatively high amounts of food to avoid depletion effects.

Our experimental set-up consisted of two sets of bottomless enclosures (one for the focal bird and one for the companion bird) placed adjacent to each other (Fig. 1). Each set had three elements: a foraging patch without any kind of protective cover (expected to be riskier for birds), a refuge patch with two pieces of artificial vegetation and three perching sites placed at different heights (expected to be safer for birds), and a link area connecting the foraging and refuge patches (Fig. 1). The circular foraging and refuge enclosures (0.5 m diameter) were 0.38 m high. Unlike previous studies in which animals were allowed to move between patches with food and patches with cover without any transition patch (Hegner 1985), our intention was to create a link separating the two patch types by some distance to recreate a travel path, which would add extra movement costs. We conducted a preliminary study, with animals that were not used in the experiment, to establish the best dimensions for a link, and found out that house finches tended to use smaller and longer links to move between patches instead of perching in them. We then used links with the following dimensions: 0.18 m × 0.18 m × 0.30 m.

Animals were free to move between patches using the link within one set, but were not allowed to move between sets. Enclosures completely made of mesh wire (opening 0.06 m, percentage open area = 85%) were placed on wooden trays with 3 cm of sawdust. We scattered 12 g of sunflower seeds in the foraging patch and covered them with a thin layer of sawdust. We left one seed visible on the substrate to prompt foraging activity, which started almost immediately irrespective of the food-deprivation level of the test subjects.

We simulated two levels of predation risk: low (before predator attack) and high (after predator attack). We used a taxidermic mount in flight position of a red-shouldered hawk, *Buteo lineatus*, as a predator. The model was suspended from a wire, which ran from 2.16 m above ground tied to the Italian stone pine tree to ground level 13.72 m away. A cord attached to a pin at the tree was pulled from outside the experimental area, which caused the hawk to fly down the wire, approaching the focal enclosure at speeds of approximately 1.71 m/s. The predator was visible to a small portion of the birds' field of view (predator exposure window) because of the placement of screens (Fig. 1). We minimized the noise of the pulley system as much as possible. During the experiments, subjects did not show any reaction to the predator before it was within the predator exposure window. Enclosure sets were placed in such a way that companions would face the predator attack before focals (Fig. 1).

During the study, we had 35 days with sunlight, and 10 days that were overcast. Owing to spatial restrictions in the area in which the experiment could be conducted, we were only able to vary light levels by placing

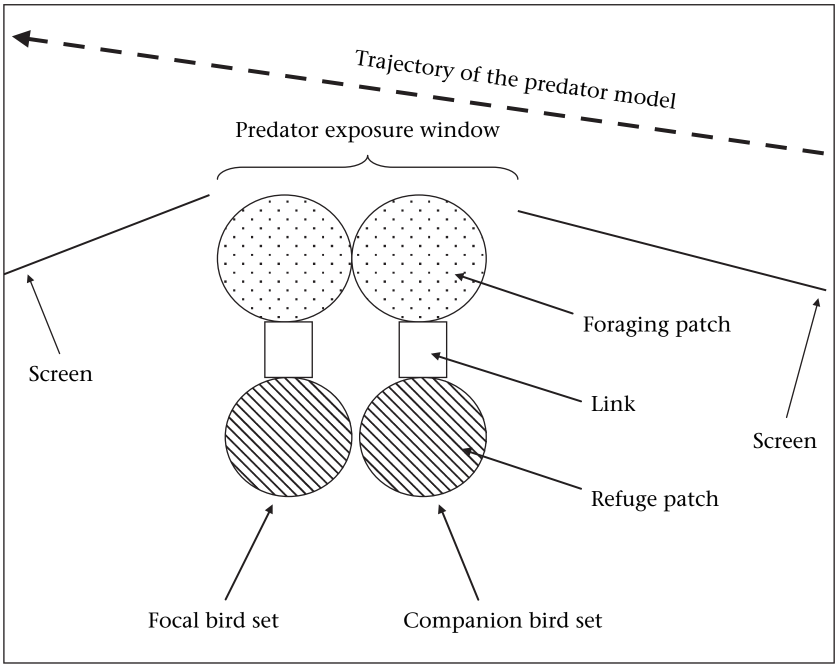

Figure 1. Schematic top-view of the experimental set-up with two sets of enclosures (foraging patch and refuge patch connected by a link) for the focal and companion house finches, showing the direction of the predator approach.

the enclosures in different spots under the Italian stone pine with different shade levels. We used the percentage of shade (estimated following Prodon & Lebreton 1981) as a proxy of light levels. In most of the trials, we were able to leave the set-up in either completely sunlit (0% shade) or shaded patches (100% shade). We could not match these differences in three trials, which had the following shade percentages: 35, 95 and 98. Since these three trials could be not lumped together into a third category, we decided to combine the 35% shade trial with the completely sunlit patches, and the other two trials (95% and 98% shade) with the completely shaded patches. Results did not vary with and without these three trials, so we decided to keep them in the analyses. Therefore, we labelled the light condition treatment as shade (low light conditions) and sunlight (high light conditions).

We measured spectrophotometrically illuminance between the two conditions with an Extech 401025 light meter. We found highly significant differences in illuminance between high and low light conditions in the focals' foraging (shade, 128.94 ± 30.21 lx; sunlight, 650.78 ± 24.67 lx; $t_{43} = 13.37$, $P < 0.001$) and refuge (shade, 146.09 ± 17.66 lx; sunlight, 498.71 ± 43.28 lx; $t_{43} = 7.24$, $P < 0.001$) patches, as well as in the companions' foraging (shade, 122.15 ± 18.36 lx; sunlight, 703.62 ± 27.42 lx; $t_{27} = 16.76$, $P < 0.001$) and refuge (shade, 163.20 ± 47.74 lx; sunlight, 494.85 ±46.22 lx; $t_{27} = 4.97$, $P < 0.001$) patches. We then considered the differences in the light conditions significant enough to expect variations in house finch behaviour.

Nevertheless, at least five confounding factors relative to light conditions could have affected bird responses: the angle of the sun relative to the horizon, sun orientation, the contrast between the predator and the background, and light reflection from the foraging substrate. The Italian stone pine tree was the only vegetation element other than grass present in our study area. However, there was no difference in the sun angle above the horizon between high and low light conditions (shade, 57.91 ± 3.87°; sunlight, 58.92 ± 1.73°; $t_{33} = 0.26$, $P = 0.792$). Similarly, sun orientation did not differ between high and low light conditions ($\chi^2_1 = 0.43$, $P = 0.511$). We moved the experimental patches to generate different shade conditions as described before, but in such a way that we kept the portion of the predator model trajectory corresponding to the predator exposure window under as much shade as possible. We also had another set of screens behind the predator to minimize potential visual contrast effects. However, in some trials, parts of the screens limiting the predator exposure window were under the sun. Nevertheless, we did not find any significant effect of the screen set-up being completely or partially under the shade ($F_{1,48} = 0.31$, $P = 0.582$), light conditions in the foraging patch ($F_{1,48} = 0.73$, $P = 0.396$), or the interaction between these two factors ($F_{1,48} = 1.08$, $P = 0.303$) on the focal's reaction time to the predator.

Finally, we measured light conditions in three types of substrates (sawdust, bare ground, grass) to assess whether illuminance in our artificial patches could be due to greater light reflection in high and low light conditions. We found significant differences between high and low light conditions (shade, 40.15 ± 1.85 lx; sunlight, 584.48 ± 9.69 lx; $F_{1,84} = 3171.09$, $P < 0.001$), but no differences between substrate types (sawdust, 317.03 ± 50.28 lx; bare ground, 318.93 ± 53.62 lx; grass, 301.00 ± 49.74 lx; $F_{2,84} = 1.38$, $P = 0.256$). Furthermore, there was no interaction between light conditions and substrate types ($F_{2,84} = 2.43$, $P = 0.090$), indicating that the lack of differences between substrates remained the same in both light conditions.

Temperature is expected to vary between both light conditions. We reduced that effect by replacing the sawdust (which had been kept at similar temperatures under a shaded area). We also checked the statistical association between light treatment and temperature for each set of enclosures (see Statistical Analysis). The frequency of trials with different light conditions did not vary from a random distribution across the levels of the different factors ($\chi^2_3 = 0.271$, $P = 0.965$).

During the study, we also varied a third condition: the social environment. We manipulated companion behaviour by food-depriving companion birds at two levels: 0.5 ± 0.12 h and 5 ± 0.12 h (for a similar approach; see Morgan 1988; Lima 1995). Companions with higher levels of food-deprivation increased their foraging behaviour (e.g. more time in the foraging patch and less time in the refuge patch; higher seed intake). We also had a control treatment in which focals foraged alone. In all of these three treatments, focal birds were food-deprived for 2.5 ± 0.12 h. In the present study, we will not focus on the social environment; however, we included it in the models to control for its potential confounding effect.

Behavioural Observations

Animals were transported from Animal Facilities to the experimental set-up in soft cloth bags and released in the enclosures (focals after companions). The observer moved away and closed the fences to avoid any external visual stimuli. Subject behaviours were recorded on two Sony DCR-TRV38 digital video cameras (one placed at 2.5 m from the focal's location, and the other, 3 m away from the refuge patches). We measured three types of behavioural responses: patch use (focal), foraging and scanning behaviour (focal), and responses to predator attack (focal and companion). We released the predator about 5 min after the start of a trial (first peck of the focal bird) while the focal was in the foraging patch, irrespective of the location of the companion. Before the predator attack, we recorded the behaviour of focals for 4.5 min. After the predator attack, we recorded focal foraging and scanning behaviours for 5 min after the focal resumed foraging. Trial duration was short enough to keep the birds foraging actively (no satiation effects) even after the predator attack. Trials were not performed in high winds or rain.

From the videotapes, we recorded patch use and foraging and scanning behaviour using an event-recording program, Jwatcher 0.9 (Animal Behaviour Laboratory, Macquarie University, Sydney, Australia) (Blumstein et al. 2000), and reaction and recovery times to predator attacks using Ulead Movie Factory 3 software (Ulead Systems Inc.l, Torrance, CA, U.S.A.) which allowed for frame-by-frame analysis.

We measured patch use by recording the proportion of time the focal bird spent in the three patch types (Fig. 1), but presented the results of the foraging patch only, because (a) the patterns in the refuge patch mirrored those in the foraging patch; and (b) focals did not spend much time in the link (one-way ANOVA: $F_{2,84} = 110.01$, $P < 0.001$, foraging patch, 72.16 ± 3.73%; refuge patch, 16.44 ±2.36%; link, 1.93 ± 4.49%). We considered that focals and companions were 'together' when they were in their foraging patches simultaneously despite the physical separation.

We established different behavioural categories to analyse foraging and scanning behaviour. A house finch could be 'on the ground' or 'off the ground' (hanging from the enclosure wall). While on the ground, it could be head-down or head-up, depending on whether its head was below or above its shoulder. While birds were with their heads up on the ground, we recorded the number and duration of scanning (no food handling) and food-handling events. Food handling in seed eaters can also be considered an indicator of scanning behaviour (Beauchamp & Livoreil 1997; Johnson et al. 2001). Since the results from scanning and food-handling behaviours were similar, we lumped both into the scanning category. We calculated the overall proportion of time scanning, scanning rate (events/min), and scan bout duration (s). While birds were head-down, we recorded the number of pecking events, and the number and duration of food-searching events (the animal was head-down but not pecking), and calculated pecking rate (events/min), and the proportion of time spent head-down searching for food.

To assess the responses to predator attacks, we measured detection time as the difference between the first appearance of the hawk within the predator exposure window (Fig. 1) and the first reaction of the focal bird (crouching or moving away, the latter encompassing flying or running) in frames. At the moment the hawk model first became visible in the predator exposure window, we also recorded whether the focal's head was under the shade or the sun, whether the companion was present in or absent from the foraging patch, and, if present, the type of companion response to the predator (crouching or moving away). While present in the foraging patch, all companions showed one of those responses to the predator either before, or, in some cases, simultaneously with the focal. We used the companion presence in the foraging patch as a criterion to study focal's detection under social conditions. There were no differences in focals' reaction time between treatments where the focal was alone in the system and those where the focal was in the foraging patch and the companion was in the refuge patch ($F_{1,19} = 0.09$, $P = 0.762$); thus, we lumped these two conditions in the companion absent category. After the initial reaction to the predator, we recorded the escape location of the focal (foraging, link, or refuge patch). We measured recovery time as the time since the focal reacted to the predator until it resumed pecking on the ground (in frames).

For each trial, we recorded body mass of focals 5 min before the trial. At the end of the trial, we sifted through the sawdust to retrieve the leftover seeds and recorded their weight to calculate seed consumption (g). E.T. performed all video analyses after extensive self-training in analysing pilot videotapes. At the time of recording the experimental tapes, for each of the main variables there was less than 5% difference between two scorings of the same trial.

Statistical Analysis

We conducted different numbers of trials per level of companion behaviour treatment (control, 15 trials; 0.5 h companion food-deprivation, 17 trials; 5 h companion food-deprivation, 20 trials). However, for patch use, foraging and scanning behaviour, and recovery time, we used 15 trials in each level of the companion behaviour treatment, because the other trials had to be interrupted 1−2 min after recording reaction times because of human disturbance. We used a different focal individual for each trial. In a given trial, each bird underwent two predation risk conditions (before and after the predator attack). Therefore, for most analyses, we conducted general linear models (GLMs) with light conditions and companion behaviour as fixed factors and predation risk as a repeated measures factor. We also included the effects of body mass (continuous), and the two-way interactions between predation risk and light conditions, and between predation risk and body mass. We ran our GLMs with overparameterized models, which were robust to unbalanced designs as well as designs with missing cells (Searle 1987; Searle et al. 1992). Some analyses (seed consumption rates, reaction and recovery times) did not include the repeated measures factor (predation risk), because we were interested in effects over the whole trial or the very responses to predators.

When analysing reaction times, we first evaluated the effects of the presence/absence of the companions in the foraging patch and light conditions. Since both factors interacted, we ran a second analysis assessing the effects of the type of companion response to the predator and whether the focal's head was under the shade or the sun on the focal's reaction time. The latter analysis was justified because glare could be limiting reaction time mainly if the eyes were exposed to high light conditions, irrespective of the light levels in the rest of the patch.

We tested whether temperature in the foraging and refuge patches was affected by light conditions (shade, sunlight) with one-way ANOVAs. Since we did not find significant associations, we presented results without the temperature effect to increase the power of our models.

We checked for normality and homoscedasticity, and transformed several variables to meet the assumptions of GLMs with log (scanning rate, scan bout duration, reaction time, and recovery time) and arcsine (proportion of time spent in the foraging patch, and proportion of time spent head-down searching for food) transformations.

Throughout, we present results as mean ± SE, using untransformed and transformed data depending on the factor studied.

We ran models to assess the effects of age and sex on all our dependent variables, and found no significant effects (all these models are available upon request), so we decided to present results without this effect.

RESULTS

Focal Patch Use

Temperature in the focal foraging ($F_{1,43} = 3.67$, $P = 0.062$; shade, 26.13 ± 0.48; sunlight, 27.37 ± 0.39) and refuge patches ($F_{1,43} = 2.73$, $P = 0.105$; shade, 26.37 ± 0.43; sunlight, 27.39 ± 0.44) did not vary significantly with light conditions, although results were close to significance. However, models including both light condition and temperature did not change the following results.

The proportion of time focals allocated in the foraging patch was affected by light conditions (Table 1): focals spent more time in the foraging patch under low than under high light conditions (arcsine-transformed: shade, 1.24 ± 0.07; sunlight, 1.01 ± 0.06). All other effects were not significant (Table 1).

Table 1. Effects of predation risk and light conditions (shaded and sunlit patches), controlling for companion food-deprivation and body mass, on the overall proportion of time spent in the foraging patch, proportion of time spent head-down searching for food, pecking rate, and seed consumption rate

	F	df	*P*
Total proportion of time spent in the foraging patch (arcsine)			
Predation risk (PR)	0.19	1,41	0.663
Light conditions (LC)	6.62	1,41	**0.014**
Companion food-deprivation (CFD)	3.02	2,41	0.059
Body mass (BM)	2.60	1,41	0.115
PR×BM	0.03	1,41	0.863
PR×LC	0.07	1,41	0.789
Proportion of time spent head-down searching for food (arcsine)			
Predation risk (PR)	0.56	1,41	0.457
Light conditions (LC)	4.23	1,41	**0.046**
Companion food-deprivation (CFD)	0.74	2,41	0.482
Body mass (BM)	0.03	1,41	0.865
PR×BM	0.55	1,41	0.461
PR×LC	0.39	1,41	0.537
Pecking rate			
Predation risk (PR)	1.20	1,41	0.279
Light conditions (LC)	7.55	1,41	**0.009**
Companion food-deprivation (CFD)	1.28	2,41	0.288
Body mass (BM)	1.86	1,41	0.181
PR×BM	1.82	1,41	0.185
PR×LC	0.48	1,41	0.492
Seed consumption rate			
Light conditions (LC)	0.57	1,40	0.453
Companion food-deprivation (CFD)	0.10	2,40	0.909
Body mass (BM)	1.26	1,40	0.268

Significant results ($P < 0.05$) are marked in bold.

Focal Behaviour in the Foraging Patch

The proportion of time spent head-down searching for food was affected by light conditions: focals decreased their foraging effort under high light conditions (arcsine-transformed: shade, 0.23 ± 0.01; sunlight, 0.18 ± 0.01, Table 1). Pecking rates were also affected by light conditions, but not by predation risk, with lower rates of pecking in high light conditions (shade, 10.62 ± 0.97; sunlight, 7.24 ± 0.79). Despite these variations in food seeking behaviour, seed consumption did not vary significantly with predation risk or light conditions (Table 1).

Regarding scanning behaviour, we found a marginally significant effect of predation risk on the proportion of time spent monitoring (including head-up scanning and food-handling) on the ground: focals increased scanning after the attack (before predator, 0.457 ± 0.024; after predator, 0.471 ± 0.027; Table 2). Furthermore, predation risk marginally interacted with body mass: the slope of the increase in time allocated to scanning with greater body mass was more pronounced before (proportion of time scanning $= -1.20 + 0.19 \times$ body mass) than after (proportion of time scanning $= 0.94 + 0.06 \times$ body mass) the predator attack (Table 2).

Table 2. Effects of predation risk and light conditions (shaded and sunlit patches), controlling for companion food-deprivation and body mass, on the proportion of time on the ground spent scanning (considering both scanning and handling behaviours), scanning rate, and scan bout duration

	F	df	*P*
Proportion of time spent scanning on the ground (arcsine)			
Predation risk (PR)	4.06	1,41	0.051
Light conditions (LC)	1.38	1,41	0.247
Companion food-deprivation (CFD)	0.70	2,41	0.501
Body mass (BM)	1.37	1,41	0.248
PR×BM	3.93	1,41	0.054
PR×LC	1.08	1,41	0.306
Scanning rate (log)			
Predation risk (PR)	3.76	1,41	0.059
Light conditions (LC)	1.35	1,41	0.253
Companion food-deprivation (CFD)	0.37	2,41	0.695
Body mass (BM)	4.16	1,41	**0.048**
PR×BM	4.31	1,41	**0.044**
PR×LC	8.54	1,41	**0.006**
Scan bout duration (log)			
Predation risk (PR)	3.00	1,41	0.091
Light conditions (LC)	10.47	1,41	**0.002**
Companion food-deprivation (CFD)	1.13	2,41	0.334
Body mass (BM)	1.82	1,41	0.185
PR×BM	2.88	1,41	0.097
PR×LC	0.12	1,41	0.727

Significant results ($P < 0.05$) are marked in bold.

Scanning rate was affected by body mass, and marginally by predation risk (Table 2). However, we detected two significant interaction effects: between predation risk and light conditions (Table 2), and between predation risk and body mass (Table 2). First, under low light conditions, there was no significant difference in scanning rate between predation risk levels (Tukey test: $P > 0.05$, Fig. 2a); however, under high light conditions, scanning rates were significantly higher before the predator attack than after it ($P < 0.05$, Fig. 2a). Second, the slope of the positive relationship between scanning rate and body mass was higher before ($\text{scanning rate} = -1.20 + 0.19 \times \text{body mass}$) than after ($\text{scanning rate} = 0.94 + 0.06 \times \text{body mass}$) the attack.

Finally, scan bout duration was only affected by light conditions (Table 2), with shorter bouts under high than under low light conditions across predation risk levels (Fig. 2b).

Focal Responses to Predator Attacks

We first assessed the effects of companion food-deprivation (control, 0.5 h and 5 h) and body mass on focals' reaction times, and found no effect (intercept, $F_{1,48} = 1.57$, $P = 0.216$; companion food-deprivation, $F_{2,48} = 0.09$, $P = 0.765$; body mass, $F_{1,48} = 0.63$, $P = 0.431$). Thus, we decided to drop them from further analyses to increase the power of our models.

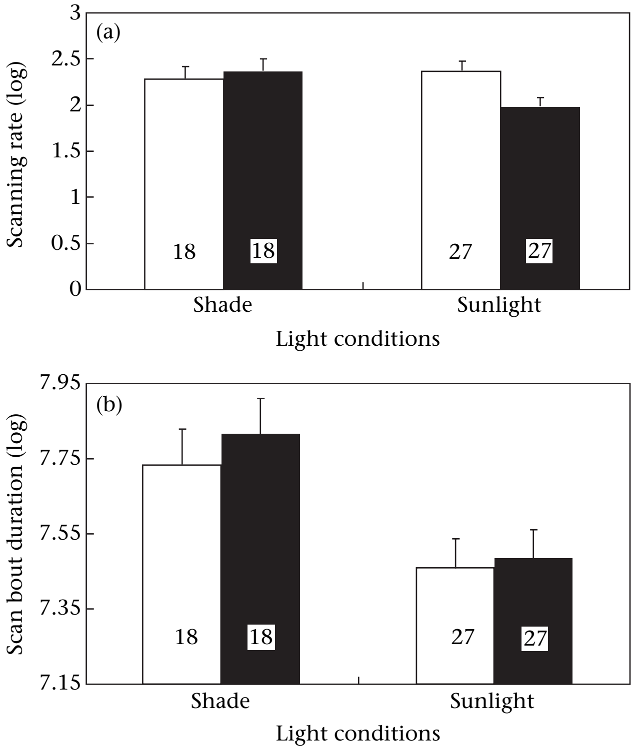

Figure 2. Focal behaviour in the foraging patch under different light levels (high, sunlit patches; and low, shaded patches) and predation risk levels (before, □, and after, ■, the predator attack): (a) scanning rate and (b) scan bout duration. Sample sizes are shown at the bottom of the bars.

We then analysed the effects of the presence of the companion at the moment of the predator attack and light conditions on focals' reaction times. We found that only the presence of companions significantly influenced reaction times (log transformed: companion present, 2.34 ± 0.10; companion absent, 1.99 ± 0.13, Table 3); however, the presence of a companion interacted with light conditions. Under low light conditions in the foraging patch, reaction times were similar irrespective of the presence or absence of a companion (Tukey test: $P > 0.05$, Fig. 3a); however, under high light conditions, reaction times were longer when the companion was present ($P < 0.05$, Fig. 3a).

The former result suggested that focals' responses could be influenced by the antipredator responses of conspecifics. Thus, we analysed the variation in focals' reaction times in relation to companion responses to the predator model (crouching or moving away), and whether focals' heads were under the shade or sunlight. Focal's reaction was longer when the companion bird crouched than when it moved away (Table 3, Fig. 3b). We also found that reaction times were longer when the focal's head was under sunlight at the moment of the attack (Table 3, Fig. 3b). However, there was no interaction between these two factors (Table 3).

Recovery times were influenced by the escape location of the focal bird and light conditions (Table 3). Focals that did not leave the foraging patch resumed foraging sooner than those that moved to the link or the refuge patch (log transformed: foraging patch, 7.13 ± 0.31; nonforaging patch, 8.39 ± 0.34). Moreover, focals took longer to return to the foraging patch under high than under low light conditions in that patch (shade, 7.29 ± 0.38; sunlight, 8.24 ± 0.26).

Table 3. Effects of the presence of the companion, light conditions (shaded and sunlit patches), companion response types (crouching, moving away), focal's head position in relation to sunlight on reaction times, and of light conditions (percentage shade) and focal's escape location (foraging, nonforaging patch) on recovery times, controlling for body mass

	F	df	P
Reaction time (log)			
Intercept	674.51	1,48	**<0.001**
Companion present/ absent (CPA)	4.56	1,48	**0.038**
Light conditions (LC)	1.31	1,48	0.257
CPA×LC	6.00	1,48	**0.018**
Reaction time (log)			
Intercept	643.18	1,28	**<0.001**
Companion response type (CRT)	6.45	1,28	**0.017**
Focal's head under shade/ light (FSHLI)	9.32	1,28	**0.005**
CRT×FSHLI	0.11	1,28	0.737
Recovery time (log)			
Intercept	1.86	1,38	0.180
Companion food-deprivation (CFD)	0.72	2,38	0.491
Escape location (EL)	8.95	1,38	**0.004**
Light conditions (LC)	4.72	1,38	**0.036**
Body mass (BM)	0.83	1,38	0.367
EL×LC	0.79	1,38	0.377

Significant results ($P < 0.05$) are marked in bold.

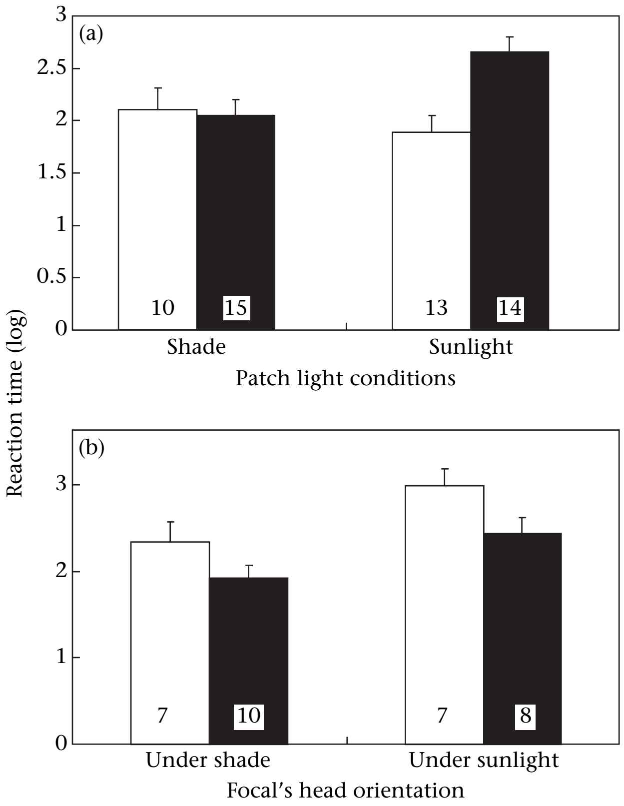

Figure 3. Focal reaction times (log transformed, in frames) towards a predator attack in two situations: (a) under high (sunlit patches) and low (shaded patches) light levels when companions were present (■) or absent (□) in the foraging patch; and (b) when focals' heads were under the shade or under the sunlight and companions responded to the predator attack by either crouching (□) or moving away (■). Sample sizes are shown at the bottom of the bars.

DISCUSSION

Heterogeneity in light conditions influenced house finch behaviour. We found that, under high light conditions in the foraging patch, focals: (a) reduced foraging patch use, (b) changed vigilance behaviour by shortening scan bout duration, (c) reduced foraging attempts, although food intake was not affected, and (d) increased the latency to detect a predator attack when foraging in pairs and when conspecifics showed antipredator responses that were more difficult to detect visually. We cannot rule out that the illuminance effect was associated with temperature, which could have increased heat stress; however, our manipulations and statistical controls suggest that temperature may have played a relatively minor role. We discuss these findings in turn.

House finches have wide visual fields (E. Fernández-Juricic, unpublished data) but lack sun shading structures (Martin & Katzir, 2000); consequently, sunlight may affect their visual detection abilities (but see alternative interpretations below). This may reduce the suitability of sunlit patches. Moreover, when foraging in sunlit patches, focals reduced the number of foraging attempts, although their intake rates were not significantly affected, probably because of the similar levels of food-deprivation across treatments.

We did not find evidence of compensatory behaviour between scanning rate and scan bout duration. Scanning rate while on the ground was not directly affected by light conditions, but it decreased after the predator under high light conditions (Fig. 2a). This could be the result of animals spending more time hanging from the wall of the enclosure to scan the surroundings for potential threats instead of staying on the ground, which has been observed before in similar experimental conditions (e.g. animals foraging in enclosures) under high predation risk (Fernández-Juricic et al. 2004b). Nevertheless, house finches did decrease the length of head-up scan bouts in high light conditions. This could be a mechanism to shorten sun exposure and decrease the chances of imaging the sun, which would degrade the contrast in the visual field (G. R. Martin, personal communication). However, the results of scanning behaviour should be interpreted with care because of the significant effects of body mass.

Shortening the duration of an average scan bout may have affected the ability of house finches to detect predators by increasing reaction times under high light conditions. This short delay in predator detection may lead to an increase in mortality, particularly with quick aerial predators (Cresswell et al. 2003; Kaby & Lind 2003; Whittingham et al. 2004; Devereux et al. 2006). Interestingly, these effects appear to be partly related to social conditions. Under low light conditions, there was no difference in the focals' reaction times with and without the presence of companions, suggesting that social benefits of antipredator strategies may be related more to dilution than to collective detection effects (Lima 1995; Fernández-Juricic & Shroeder 2003; but see Powell 1974; Roberts 1997; Cresswell et al. 2001). This could be the result of animals not paying attention to the levels of vigilance of conspecifics (Lima & Zollner 1996; Beauchamp 2002). However, under high light conditions, reaction times when foraging alone were similar to those found under low light conditions, but increased when foraging in pairs (Fig. 3). A possible explanation is that companions were closer to the predators during the attacks (Fig. 1), which may have reduced focals' perceived risk of capture, and hence the need to escape quickly. However, these effects only took place under high light conditions. Thus, animals may have paid attention to the escape behaviour of conspecifics, but the transmission of this antipredator social information may have been constrained because of light intensity. Because there was no change in the proportion of time spent scanning between solitary and social conditions (see companion food-deprivation effect in Table 2), we suggest that focals switched the targets of scanning to companions, as found in recent studies with starlings, *Sturnus vulgaris* (Fernández-Juricic et al. 2004b, 2005). Future empirical consideration should be focused on establishing the relative use of personal versus social information in different light conditions as well as the effects of light contrasts between the predator and the prey, which were minimized in this study but could have a major effect on predator detection abilities.

When animals foraged in pairs, reaction times varied with the type of escape response of companions. Focals would reduce the chances of being caught by a predator by detecting different companion responses at the same time and reacting immediately afterwards. However, reaction times were longer when companions crouched, which would be more difficult to detect than when companions moved away from the predator. This constraint in the transmission of social information is expected to be enhanced under high light conditions, but we did not find any significant interaction effect. Taken together, these findings underscore the complexity of the visual environment (and the associated responses) when birds forage in groups under varying illuminance.

Overall, high illuminance increased the costs of predator detection probably through sun imaging, which may partially explain why animals shunned from exploiting sunlit patches. Observational studies also suggest that some Neotropical forest birds avoid high light conditions by foraging lower in the foliage and closer to the trunk (Walther 2002). However, the avoidance of sunlit patches may well be accounted for by other factors. First, animals standing in sunlit patches may be more visible to predators than when in the shade, increasing their perceived predation risk. Second, in sunlit patches, it may be more difficult not only to detect predators (with personal and social information) but also to detect food, because of light reflection from the ground. However, we did not find that our artificial foraging substrate increased light reflection significantly in relation to natural foraging substrates or that intake rates were affected in any significant way. Third, the observed effects may be generated by transitions when eyes go from sunny to shaded areas (and vice versa) instead of sun imaging per se.

Our results indicate a new ecological factor influencing foraging behaviour and predation risk: heterogeneity in light conditions. If other species respond similarly, and if our effects scale up to the level of the flock, we predict that birds exploiting habitats with heterogeneous light conditions would reduce the time spent in sunlit patches if the costs of gathering personal and social information relative to predation risk are higher than the benefits from compensatory mechanisms to maintain high detection levels. Some compensatory mechanisms in sunlit patches may include: (a) an increase in scanning rate with a decrease in scan bout duration, (b) an increase in group size to dilute predation risk, (c) a reduction in neighbour distances that would ensure the quick transmission of social antipredator information, and (d) changes in head orientation to avoid imaging the sun by orienting the blind areas of the visual fields towards the sun or by positioning the head during scan bouts in such a way that the sun's image falls upon the pecten (G. R. Martin, personal communication). The pecten is a small area within the peripheral retina with dense black pigmentation that could absorb the sun image and reduce light scattering within the eye. These predictions could be tested in habitats with heterogeneous light conditions (e.g. forest edges, savannas, etc.) and in bird species without sun-shading structures (Martin & Katzir, 2000).

Acknowledgments

This study was supported by the College of Natural Sciences and Mathematics (California State University Long Beach) and Howard Hughes Medical Institute grant no. 52002663. We thank Guy Beauchamp, Graham Martin, Anna Valcarcel, and Rachael Poston for fruitful discussions on an earlier draft, two anonymous referees, Will Cresswell, and Dan Papaj, for constructive criticism, Robert Cummings, Jim Web, Valerie Nguyen, Chase McDonald, and Nima Gilak for their help during the experiments, and Alan Miller and Kevin Kelly for their encouragement to pursue this study.

References

Beauchamp, G. 1998. The effect of group size on mean food intake rate in birds. *Biological Reviews*, **73**, 449–472.

Beauchamp, G. 2002. Little evidence for visual monitoring of vigilance in zebra finches. *Canadian Journal of Zoology*, **80**, 1634–1637.

Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes*, **63**, 111–121.

Beauchamp, G. & Livoreil, B. 1997. The effect of group size on the vigilance and feeding rate in spice finches (*Lonchura punctulata*). *Canadian Journal of Zoology*, **75**, 1526–1531.

Beauchamp, G. & McNeil, R. 2003. Vigilance in greater flamingos foraging at night. *Ethology*, **109**, 511–520.

Bednekoff, P. A. & Lima, S. L. 2005. Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? *Animal Behaviour*, **69**, 1165–1171.

Blumstein, D. T., Evans, C. & Daniel, J. C. 2000. *JWatcher 0.9*. Available from: http://galliform.psy.mq.edu.au/jwatcher/.

Brown, M. B. & Brown, C. M. 1988. Access to winter food resources by bright-versus dull-colored house finches. *Condor*, **90**, 729–731.

Cook, R. G. 2001. *Avian Visual Cognition*. Available from: www.pigeon.psy.tufts.edu/avc/.

Cresswell, W. & Whitfield, D. P. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, south-east Scotland. *Ibis*, **136**, 223–232.

Cresswell, W., Hilton, G. M. & Ruxton, G. D. 2001. Evidence for a rule governing the avoidance of superfluous escape flights. *Proceedings of the Royal Society of London, Series B*, **267**, 733–737.

Cresswell, W., Lind, J., Kaby, U., Quinn, J. L. & Jakobsson, S. 2003. Does an opportunistic predator preferentially attack nonvigilant prey? *Animal Behaviour*, **66**, 643–648.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, **20**, 187–193.

Danchin, E., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public information: from noisy neighbors to cultural evolution. *Science*, **305**, 487–491.

Devereux, C. L., Whittingham, M. J., Fernández-Juricic, E., Vickery, J. A. & Krebs, J. R. 2006. Predator detection and avoidance by starlings under differing scenarios of predation risk. *Behavioral Ecology*, **17**, 303–309.

Dukas, R. 1998. Constraints on information processing and their effects on behavior. In: *Cognitive Ecology* (Ed. by R. Dukas), pp. 89–128. Chicago: Chicago University Press.

Dukas, R. & Kamil, A. C. 2000. The cost of limited attention in blue jays. *Animal Behaviour*, **11**, 502–506.

Fernández-Juricic, E. & Kacelnik, A. 2004. Information transfer and gain in flocks: the effects of quantity and quality of social information at different neighbour distances. *Behavioral Ecology and Sociobiology*, **55**, 502–511.

Fernández-Juricic, E. & Schroeder, N. 2003. Do variations in scanning behaviour affect tolerance to human disturbance? *Applied Animal Behaviour Science*, **84**, 219–234.

Fernández-Juricic, E., Erichsen, J. T. & Kacelnik, A. 2004a. Visual perception and social foraging in birds. *Trends in Ecology & Evolution*, **19**, 25–31.

Fernández-Juricic, E., Siller, S. & Kacelnik, A. 2004b. Flock density, social foraging and scanning: an experiment with starlings. *Behavioral Ecology*, **15**, 371–379.

Fernández-Juricic, E., Smith, R. & Kacelnik, A. 2005. Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. *Animal Behaviour*, **69**, 73–81.

Giraldeau, L.-A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Giraldeau, L.-A., Valone, T. J. & Templeton, J. J. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 1559–1566.

Hegner, R. E. 1985. Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). *Animal Behaviour*, **33**, 762–768.

Hilton, G. M., Cresswell, W. & Ruxton, G. D. 1999. Intraflock variation in the speed of escape-flight response on attack by an avian predator. *Behavioral Ecology*, **10**, 391–395.

Hutchinson, J. M. 2002. Two explanations of the dawn chorus compared: how monotonically changing light levels favour a short break from singing. *Animal Behaviour*, **64**, 527–539.

Johnson, C. A., Giraldeau, L.-A. & Grant, J. W. A. 2001. The effect of handling time on interference among house sparrows foraging at different seed densities. *Behaviour*, **138**, 597–614.

Kaby, U. & Lind, J. 2003. What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behavioral Ecology and Sociobiology*, **54**, 534–538.

Kacelnik, A. 1979. The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Animal Behaviour*, **27**, 237–242.

Kendal, R. L., Coolen, I. & Laland, K. N. 2004. The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, **15**, 269–277.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.

Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, **49**, 11–20.

Lima, S. L. & Zollner, P. A. 1996. Anti-predatory vigilance and the limits of collective detection: visual and spatial separation between foragers. *Behavioral Ecology and Sociobiology*, **38**, 355–363.

Lind, J. & Cresswell, W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945–956.

Martin, G. R. & Katzir, G. 2000. Sun shades and eye size in birds. *Brain Behaviour and Evolution*, **56**, 340–344.

Morgan, M. J. 1988. The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. *Animal Behaviour*, **36**, 1317–1322.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, **22**, 501–505.

Prodon, R. & Lebreton, J. D. 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. *Oikos*, **37**, 21–38.

Roberts, G. 1997. How many birds does it take to put a flock to flight? *Animal Behaviour*, **54**, 1517–1522.

Searle, S. R. 1987. *Linear Models for Unbalanced Data*. New York: J. Wiley.

Searle, S. R., Casella, G. & McCullock, C. E. 1992. *Variance Components*. New York: J. Wiley.

Shedd, D. H. 1990. Aggressive interactions in wintering house finches and purple finches. *Wilson Bulletin*, **102**, 174–178.

Templeton, J. J. & Giraldeau, L.-A. 1995. Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behavioral Ecology*, **6**, 65–72.

Thomas, R. J., Székely, T., Cuthill, I. C., Harper, D. G. C., Newson, S. E., Frayling, T. D. & Wallis, P. D. 2002. Eye size in birds and the timing of song at dawn. *Proceedings of the Royal Society of London, Series B*, **269**, 831–837.

Thomas, R. J., Kelly, D. J. & Goodship, N. M. 2004. Eye design in birds and visual constraints on behavior. *Ornitologia Neotropical*, **15**, 243–250.

Valone, T. J. & Templeton, J. J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 1549–1557.

Walther, B. A. 2002. Vertical stratification and use of vegetation and light habitats by neotropical forest birds. *Journal für Ornithologie*, **143**, 64–81.

Whitfield, D. P. 2003. Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *Journal of Animal Ecology*, **72**, 27–35.

Whittingham, M. J., Butler, S. J., Quinn, J. L. & Cresswell, W. 2004. The effect of limited visibility on vigilance behavior and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos*, **106**, 377–385.