



# 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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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.

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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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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

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