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A dynamic method to study the transmission of social foraging information in flocks using robots

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To understand the mechanisms underlying the flow of social information in foraging groups, it is important to manipulate the behaviour of individuals and study the responses of flock members under different ecological and social conditions. Some studies have attempted this using three-dimensional models, like robots. Our goal was to assess the foraging and scanning behaviour of adult house finches, *Carpodacus mexicanus*, in response to robots mimicking different types of behaviours in artificial flocks (three linearly placed enclosures, with robots at the periphery and a live animal at the centre). We recorded whether live animals reacted to (1) the presence/absence of robots, (2) the motion of robots in relation to static robots, (3) variations in the type of robot behaviour and (4) the direction of the responses (increasing or decreasing their foraging effort). Adult house finches reacted differently to the presence, motion and behaviour of robots, and they spent more time foraging and less time scanning, which led to increasing seed intake, as the robots simulated body movement that could be associated with successful foraging behaviour (more handling time) or antipredator behaviour. Responses to robots were similar to those given to live conspecifics. We discuss advantages and disadvantages of using robots in social foraging research and conclude that robots are suitable to test some hypotheses on the foraging and antipredator behaviour of flocks.

Animals need information to make foraging and antipredator decisions. Information can be gathered through personal monitoring of different targets (predators, food patches) and/or through monitoring conspecifics if animals gather in groups. How social information (information that goes from one group member to the next) is transmitted across a group has attracted theoretical and empirical attention (reviewed in Bednekoff & Lima 1998; Treves 2000; Giraldeau et al. 2002; Valone & Templeton 2002; Fernández-Juricic et al. 2004a). For instance, the distance separating group members could affect the speed with which a predator is detected (Hilton et al. 1999) and the flow of information relative to foraging opportunities (Fernández-Juricic et al. 2004b), and, as a result, the chances of surviving a predator attack and avoiding starvation. Given the importance of social information for fitness-related parameters, understanding its mechanisms of transmission in animal groups would allow us to better predict the behaviour of individuals in groups under different ecological conditions (Beauchamp 2003a, b).

Despite the plethora of empirical research on social foraging (reviewed in Beauchamp 1998; Giraldeau & Caraco 2000; Krause & Ruxton 2002), studying the mechanisms of social information transmission has been challenging, because it is sometimes difficult to conduct controlled experiments that make it possible to uncover cause–effect relationships and to manipulate the behaviour of flock members and assess the reaction of test subjects. The scope of observational studies is constrained by many confounding factors (Elgar 1989; Beauchamp 1998; Treves 2000); however, some laboratory experiments (e.g. Templeton 1998; Coolen et al. 2001; Beauchamp 2002) and seminatural experiments (e.g. Lima 1995; Templeton & Giraldeau 1995; Fernández-Juricic & Kacelnik 2004) can yield information on causation under controlled conditions (e.g. marked individuals, similar food-deprivation levels). Some studies have attempted to manipulate social information with live animals (e.g. Fernández-Juricic & Kacelnik 2004), but their utility is limited because the behaviour of animals acting as senders

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could also be affected by the responses of animals acting as receivers. An alternative way of manipulating social information is by using artificial models.

The use of models has been common in animal behaviour (e.g. Lack 1943; Tinbergen & Perdeck 1950; Stout & Brass 1969). Three studies to date have used artificial models to analyse aspects of social foraging information transmission. The presence of a large number of head-up painted styrofoam models of great blue heron, *Ardea herodias*, in a foraging patch increased the chances that live flying animals would land and forage near them (Krebs 1974), suggesting that animals cue in on the number of conspecifics to make patch selection decisions. Another study using painted fibre glass models in two body postures (head-up and head-down), showed that barnacle geese, *Branta leucopsis*, increased the probabilities of landing and staying longer in patches with a higher proportion of head-down artificial models (Drent & Swierstra 1977). This result suggests that body postures of conspecifics mimicking foraging behaviour could be used as cues to select foraging patches. Finally, in a recent study to assess developmental responses to social cues conducted in an aviary, using robots made of taxidermic mounts, Australian brush-turkey, *Alectura lathami*, chicks preferred a pecking model over static or scanning models (Göth & Evans 2004). This result suggests that social responses of chicks depend upon conspecific motion patterns, even though this species does not frequently form cohesive flocks. Using robots to manipulate the behaviour of conspecifics could enhance our ability to investigate the mechanisms of social transmission in flocks (for examples of the use of robots in other contexts, see Webb 2001; Patricelli et al. 2002; Partan 2004; Martins et al. 2005). Other studies have used two-dimensional stimuli (videos and pictures; e.g. D'eath 1998; Delius et al. 1999; Jitsumori et al. 1999; Ophir & Galef 2003), but we believe that robots can be more useful than these stimuli, because they are three-dimensional, real-time models whose behaviour can be complex but precisely controlled.

To assess the utility of robots for social foraging research, it is important to test whether they would elicit foraging responses of adult birds of social species under conditions similar to the ones that they experience in natural foraging grounds. Our goal was to assess different parameters of the foraging and scanning behaviour of live house finches, *Carpodacus mexicanus*, to variations in the absence and presence of robots displaying different types of foraging behaviours. We also assessed the birds' responses to live flockmates showing similar behavioural patterns to the robots. We tested four questions. (1) Do live animals react differently to the presence/absence of robots? (2) Do live animals modify their behaviour in response to the motion of robots in relation to static robots? (3) Do live animals react to variations in the type of robot behaviour? (4) Are responses to robots similar to those given to live individuals? We generated two types of robot behaviour: short head-up bouts, which could mimic unsuccessful pecking attempts, and long head-up bouts, which could mimic successful foraging attempts resulting from increased handling time. Longer duration of head-up bouts in this species can also be associated with an increase in scanning behaviour; thus, we predicted two possible outcomes. Live animals could increase foraging efforts with an increase in robot head-up time because they copy apparently successful foraging behaviour of robots (e.g. higher value of foraging patches), or they could decrease foraging efforts because higher robot monitoring is associated with increasing predation risk.

METHODS

General Sampling Procedures

We conducted the study at California State University, Long Beach (CSULB) campus from 17 September to 6 December 2004, on a grassy area shaded by an old tree. This area was 25 m away from the closest pathway, which received low pedestrian traffic, so noise levels were minimized. The area was also surrounded by 1.80 m of fencing covered with black plastic and black cloth to screen out external visual stimuli.

We caught and colour-ringed 105 adult house finches belonging to four populations in southern California: Seal Beach, Bolsa Chica, Irvine and Fullerton. Animals were housed in indoor cages ($0.85 \times 0.60 \times 0.55$ m), 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. A veterinarian and trained personnel supervised daily the animals' health. All experimental protocols were approved by the Animal Welfare Board at CSULB (Protocol no. 206).

Our original intention was to use a repeated measures design, in which each subject could be exposed to the different treatment conditions, which meant keeping the animals in captivity for at least 2 months because they would be assigned randomly to different treatments. However, in preliminary trials to test bird housing in captivity, mortality was up to 35% after 48 h; most of the deaths were caused by head trauma. Therefore, for ethical reasons and following the recommendations of the CSULB Animal Welfare Board, we changed our design by capturing a bird, testing it only once the next day, and releasing it within 48 h in the same location where it had been captured. This approach increased bird survival to 100% and was adopted for the present study (see also Whittingham et al. 2004). Consequently, each data point corresponds to a different individual. Animals belonging to different populations were assigned randomly to the different treatments. The proportion of trials with males and females did not differ from a random distribution across the different treatments in either the robot experiment (chi-square test: $\chi^2_3 = 1.84$, $P = 0.607$) or in the experiment including all live individuals ($\chi^2_3 = 0.42$, $P = 0.515$).

We assessed the reaction of live animals to robots in seminatural conditions, on areas that house finches generally use to forage on campus, but controlling certain factors such as identity of the subject, food-deprivation