



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.

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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'eaath 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 × 0.60 × 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

time, time available to forage, food availability, distance between live animals and robots, and number of individuals in the flock. This seminatural approach has proven useful to answer questions about social foraging mechanisms (Smith 2002; Fernández-Juricic et al. 2004b). Maintaining conditions as natural as possible is relevant, because house finches substantially change their behaviour when foraging in indoor locations (e.g. aviary or laboratory), apparently because animals do not expect predation events (E. Fernández-Juricic, unpublished data). From comparisons with observational data obtained from wild populations, we determined that the foraging and scanning behaviour of house finches in our seminatural set-up was representative of natural conditions.

We used three bottomless enclosures (0.50 m diameter) made of mesh wire (opening 0.06 m, percentage open area = 85%), placed on wooded trays with 3 cm of sawdust. We scattered 7 g of sunflower seeds and covered them with sawdust. Enclosures were arranged linearly, with the live bird at the centre and the robots at the periphery of the flock. Enclosures were separated by 1 m.

Robots were built using two skin specimens (one male and one female) that were decommissioned from the Museum of Ornithology at CSULB (Fig. 1). We chose specimens from southern California populations to minimize biases associated with geographical variations in coloration (Hill 1993). Robots were designed and built in collaboration with Mod-L-Mania Custom Applications (Long Beach, California). We inserted a microservo (Futaba S3108) into the cavity of the specimen and secured it with silicon glue (Fig. 2a). We eliminated the logic portion of the microservo circuit and shielded the motor with

phone tape to minimize noise that could affect the behaviour of live animals. A servo horn was inserted into a 3-cm-long metal tube (Fig. 2a), which was used as the pivot point from the bird to generate movement between two body positions, head-up and head-down (Fig. 1). We then secured the metal tube to the wooded base of the enclosure and covered the bottom of the base with Kaytee Aspen Bedding during the trials. An 8-m e-pin connection cable (20 gauge) connected each microservo to a control box with two printed circuit boards (IBM-007, OWI Robot Arm Kit, Carson, California), a function board and a logic board (Fig. 2b). We used RCA phone jacks to connect the cables to the control box. Four D batteries powered the microservos and the control box, which was connected with a 232 serial cable to an Enpower laptop ENP-312 + PC (AMD-K6 3D Processor, 32 MB RAM) with Microsoft Windows 98 operating system. The control box and the laptop were outside of the fenced experimental area. The durations of head-up and head-down body postures of the robots were controlled with the OWI Robot software (PC Interface Robotic Arm Trainer Ver 1.0, Carson, California). It took robots 490 ms to change positions. The movements of the two robots were synchronized so that they performed the same behaviours almost simultaneously.

We measured the behavioural responses of live house finches in four treatment conditions. First, the bird foraged without robots but with the peripheral enclosures surrounding it (no robot treatment). Second, the bird foraged with immobile robots: one of the robots was head-up and the other one head-down during the whole trial (immobile robots treatment). We randomized the position (right or left) and sex of the robot in each posture in each



Figure 1. Robots used in the experiment built from male and female house finch skins. The picture shows robots in head-up position, the metal tubes that were used to pivot the robots, the wooded base of the enclosure without the bedding, and the control box that was connected to a laptop to control the frequency of head-up and head-down postures. This picture does not show the robots in the experimental set-up.

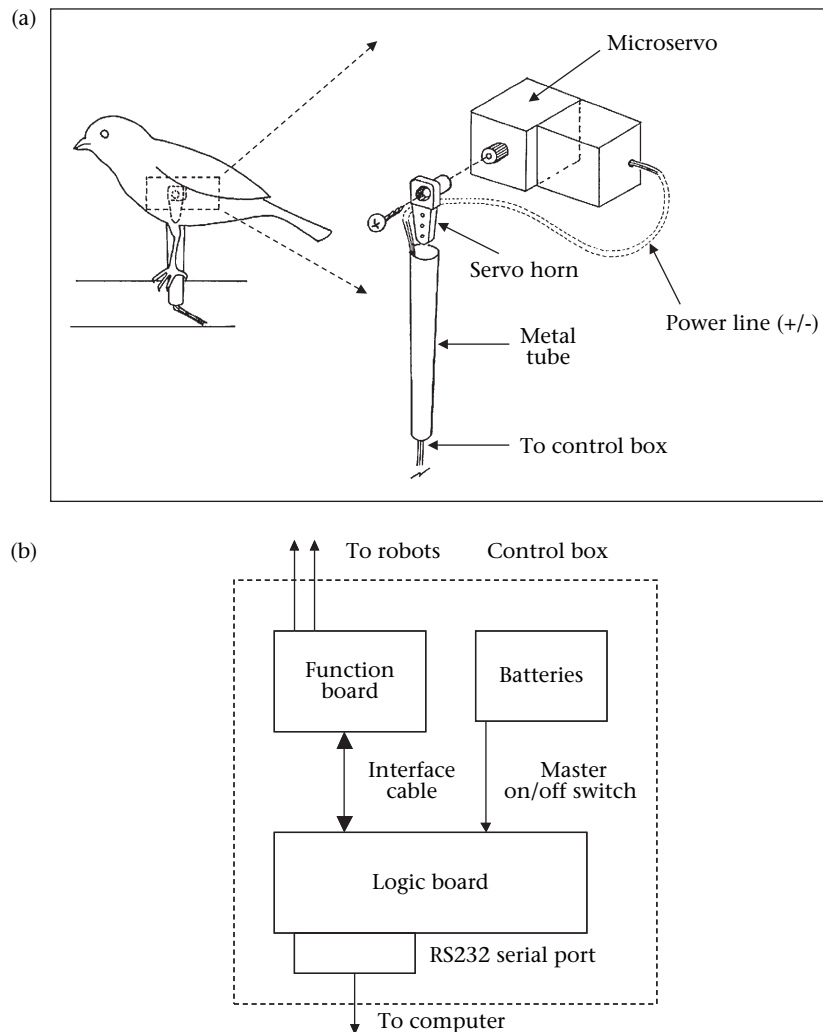


Figure 2. Schematic representation of the mechanism controlling the robots. (a) A microservo was inserted within the skin and connected through a servo horn to a metal tube. (b) The control box consisted of a function board or terminal connector (Robotic Arm Part no. 43), a logic board or control PC board (Robot Arm Part no. 44), four D batteries, and a serial port that connected to a laptop computer.

trial. These two treatments served as controls to assess whether birds reacted differently to the presence and motion of robots. We created two other treatments in which the robots simulated two different behaviours, which were based on observations of the behaviour of wild birds in natural conditions. We determined that the mean \pm SE duration of a bout of seed handling was 4220 ± 3880 ms. In the first treatment, robots remained head-up for 500 ms and then head-down for 1700 ms, and the sequence was repeated until the end of the trial. This treatment mimicked an unsuccessful food-searching behaviour (short head-up bouts). In the second treatment, robots remained head-down for 450 ms and then head-up for 6250 ms, and the sequence was repeated until the end of the trial. This treatment mimicked a head-down behaviour followed by head-up food-handling behaviour or a long monitoring bout (long head-up bouts).

Birds were food deprived 3–4 h before trials. Animals were transported from Animal Facilities to the experimental set-up in soft cloth bags and released into the enclosures. The observer moved away and closed the fences to

avoid external visual stimuli. The behaviour of the focal bird was recorded on a Sony DCR-TRV38 digital video camera placed 2.5 m from the focal bird's location. One problem with experiments involving robots is that animals may habituate to robots relatively quickly (Göth & Evans 2004). We ran preliminary tests with six birds, which were not later used in this experiment, exposing them to robots for 45 min. We found a sharp change in some behaviours indicative of habituation to the robot (i.e. decrease in foraging effort and increase in time spent in activities not related to foraging, such as wall hanging) after a mean \pm SE of 26.39 ± 8.57 min after the first peck by the focal bird. To be conservative, we used 10-min trials, timed from the first peck by the focal bird. Trial duration was short enough to keep the birds foraging actively (i.e. no satiation effects) and to avoid food depletion. Trials were not performed in high winds or rain.

To assess whether the responses to robots were similar to those given to live flockmates, we carried out another experiment with the same general procedures and set-up as described before, but with two live peripheral

conspecifics separated by 1 m from the central focal bird. Focal birds were food deprived for a mean \pm SE of 150 ± 20 min before the trials and received 7 g of sunflower seeds in all treatments. We manipulated two conditions: (1) both peripheral conspecifics were food deprived for 240 ± 20 min and were provided with 0.5 g of sunflower seeds, and (2) both peripheral conspecifics were not food deprived and were provided with 7 g of seeds. Condition 1 increased food-searching behaviour by conspecifics and reduced head-up bout duration (short head-up bouts), whereas condition 2 reduced food searching and increased head-up bout duration (long head-up bouts). Trials also lasted 10 min from the first peck by the focal bird.

The behaviour of focal house finches was recorded from videotapes using an event-recording program (Jwatcher 0.9; Blumstein et al. 2000). We based our analysis on variations in the behaviour of house finches in the enclosures. A house finch could be 'on the ground' or 'off the ground' (hanging from the enclosure wall). While on the ground, the bird could be either head-down or head-up, depending on whether its head was below or above its shoulder. House finches handled food from different positions (head-up and head-down on the ground, and hanging from the enclosure walls). While the birds had their heads up on the ground, we recorded the number and duration (s) of scanning events (i.e. no food handling) and food-handling events. We also recorded the number of times and the time (s) spent off the ground (i.e. hanging from the enclosure walls) with and without food handling, because this behaviour has been associated with monitoring objects that are difficult to spot from the ground position (Fernández-Juricic et al. 2004b). In defining our dependent variables while the birds were on the ground, we used the term 'scanning' based on the descriptive operational definition of having the head-up, but we also classified times off the ground as scanning, because in this way the label reflected all the times that were definitely not available for direct food finding. While the bird was head-down, we recorded the time spent head-down, number of pecking events, the number and duration of food-searching events (i.e. the animal was head-down but not pecking), and number and duration of food-handling events. We then calculated the proportion of time scanning (including on and off the ground), scanning rate and scanning bout duration (including on and off the ground), proportion of time spent head-down, food-searching rate, food search bout duration, pecking rate and food-handling bout duration (including head-up and head-down on the ground).

For each trial in the robot experiment, we recorded ambient temperature, body mass of the focal bird 5 min before the trial, and the time that the focal bird was food deprived. At the end of the trial, we sifted through the sawdust to retrieve the leftover seeds and recorded their weight (g) to calculate seed consumption. In the experiment with live peripheral conspecifics, we measured ambient temperature and body mass of the focal bird 5 min before the trial, and kept food-deprivation times within the ranges specified in the design for each individual, as described above.

Video analyses were performed by P.P. in the robot experiment and by A.V. in the live conspecifics experiment after extensive self-training. At the time of recording the experimental tapes, for each of the main variables, there was less than a 5% difference between two scorings of the same tape.

Statistical Analysis

In the robot experiment, we included 63 trials corresponding to four treatments: no robots ($N = 15$ trials), immobile robots ($N = 16$ trials), robots with short head-up bouts ($N = 17$ trials) and robots with long head-up bouts ($N = 15$ trials). The different number of trials per treatment yielded an unbalanced design. We compared the output of the statistical analyses between the unbalanced design and different balanced designs ($N = 15$ trials per treatment) by randomly choosing 15 trials in those treatments with more samples; we found no differences in the results (data available from the authors upon request). There was no significant correlation between the three independent continuous factors (ambient temperature, body mass and food-deprivation time; Pearson correlation: $r = 0.08$ – 0.17 , all $P_s > 0.05$).

We used general linear models to analyse nine dependent variables (seed consumption, proportion of time spent head-down, food-searching rate, food search bout duration, pecking rate, food-handling bout duration, proportion of time scanning, scanning rate, scanning bout duration), including treatment (no robot, immobile robot, robots with short head-ups, robots with long head-ups) and sex as categorical independent factors, and temperature, body mass and food-deprivation time as continuous independent factors. Our design was unbalanced, so we ran the general linear models with overparameterized models, which are robust to unbalanced designs as well as to designs with missing cells (Searle 1987; Searle et al. 1992). We checked variables for normality and homoscedasticity, and arcsine-transformed the proportion of time spent head-down.

We first report the results of the overall general linear model, then answer the first three questions posed in the Introduction using planned comparisons (Rosenthal & Rosnow 1985). To assess whether animals reacted differently to the presence or absence of robots, we compared the no-robot treatment versus the combination of treatments using an immobile robot and robots with short and long head-up bouts. To determine whether animals modified their behaviour in relation to the motion of robots, we compared the immobile robot treatment versus the combination of treatments using robots with short and long head-up bouts. Finally, to evaluate whether animals responded to variations in the type of robot behaviour, we compared between-robot treatments using short and long head-up bouts.

Some of the dependent variables describing foraging and scanning performance are interdependent (e.g. the proportion of time spent head-down could be associated with the proportion of time scanning), so the results cannot be combined for hypothesis testing. In spite of

this, we conducted statistical analyses on many variables to achieve quantitative measurements of the effects of the robots along several foraging and scanning dimensions to understand the behavioural mechanisms related to the responses to robots. We assumed that pecking was an indicator of successful foraging effort. We found a strong positive relationship between pecking rate and food-handling rate across treatments (Pearson correlation: $r_{61} = 0.78$, $P < 0.001$), which corroborated that assumption.

In the experiment with actual peripheral conspecifics, our design was balanced ($N = 7$ trials in each treatment). We used a general linear model including treatment (short and long head-up bouts) as the categorical independent factor, and body mass and ambient temperature as the continuous independent factors. Body mass and ambient temperature were not correlated (Pearson correlation: $r_{61} = 0.15$, $P = 0.605$). The proportion of males in each treatment was low, so we could not include sex in the final model. We analysed the two most sensitive behavioural responses to robots (see Results): (arcsine) proportion of time spent head-down and (log) pecking rate, which were transformed to meet model assumptions. Throughout, we report means \pm standard errors.

RESULTS

Experiment with Robots

Despite focal birds having the same amount of food available, seed consumption varied significantly between the four treatments (Fig. 3a), with no detectable effect of the confounding factors (Table 1). House finches ate more seeds when robots were present (GLM: $F_{1,52} = 8.19$, $P = 0.006$), and when robots were moving than when robots were immobile ($F_{1,52} = 12.28$, $P < 0.001$). Finally, seed consumption was higher when robots increased the duration of head-up bouts ($F_{1,52} = 7.45$, $P = 0.009$).

The proportion of time that house finches spent head-down differed between treatments (Table 1, Fig. 3b). Focal birds spent more time head-down in the presence of robots ($F_{1,52} = 36.52$, $P < 0.001$) and when robots were moving in relation to immobile robots ($F_{1,52} = 8.49$, $P < 0.005$). House finches spent more time head-down when robots increased head-up bout duration ($F_{1,52} = 4.25$, $P = 0.044$). Food-searching rate varied between treatments ($\bar{X} \pm$ SE events per min: no robot: 1.98 ± 0.57 ; immobile robots: 2.45 ± 0.55 ; robots with short head-up bouts: 3.72 ± 0.54 ; robots with long head-up bouts: 4.11 ± 0.56 ; Table 1), increasing with the presence of robots (GLM: $F_{1,52} = 4.86$, $P = 0.031$) and when robots were moving ($F_{1,52} = 4.71$, $P = 0.034$). However, we found no significant differences in food-searching rate between robots with different head-up bout durations ($F_{1,52} = 0.24$, $P = 0.627$). Food search bout duration differed between treatments (no robot: 0.436 ± 0.066 s; immobile robots: 0.685 ± 0.064 s; robots with short head-up bouts: 0.748 ± 0.063 s; robots with long head-up bouts: 0.706 ± 0.065 s; Table 1). However, this difference was mainly due to the presence of robots ($F_{1,52} = 13.14$, $P < 0.001$), because we found no difference

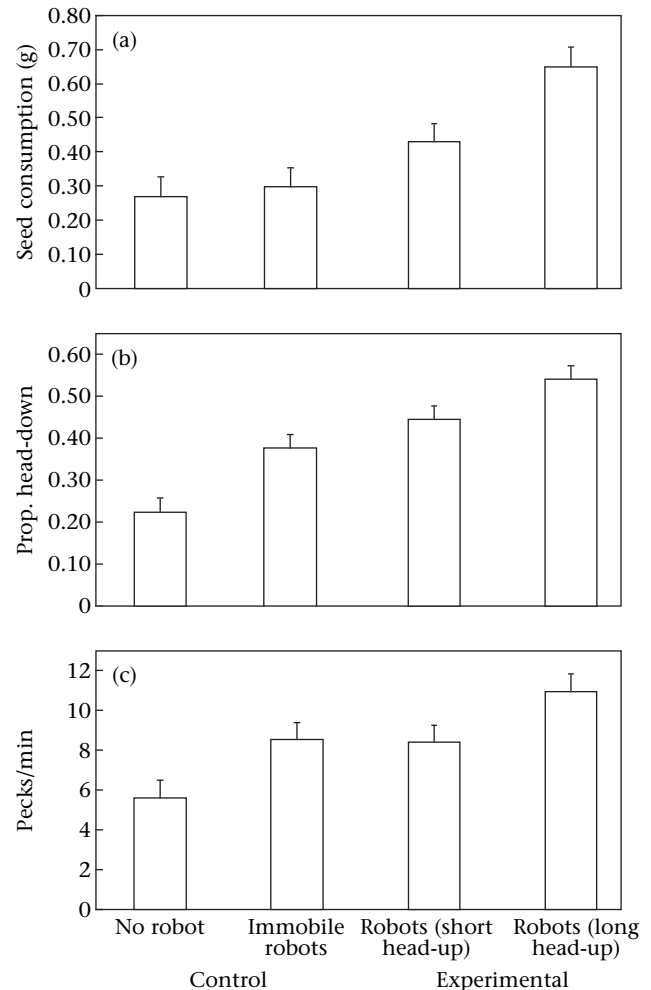


Figure 3. Foraging responses (a: seed consumption rate; b: proportion of time spent head-down; c: pecking rate) of house finches to the presence and behaviour of two robots. Control treatments included either the absence of robots in the enclosures (no robots), or the presence of immobile robots in the enclosures (one in a head-up posture and the other in a head-down posture). In the two experimental treatments, the body postures of robots were modified in time to generate two conditions: short head-up bouts (unsuccessful foraging) and long head-up bouts (successful foraging).

between immobile and moving robots ($F_{1,52} = 0.29$, $P = 0.599$) or between robot foraging with different head-up bout durations ($F_{1,52} = 0.19$, $P = 0.657$).

Pecking rate varied significantly between treatments (Table 1, Fig. 3c). Focals increased pecking rate with the presence of robots (GLM: $F_{1,52} = 13.46$, $P < 0.001$), but the differences between robots with and without motion were not significant ($F_{1,52} = 1.17$, $P = 0.284$). However, pecking rate increased when robots increased the duration of head-up bouts ($F_{1,52} = 4.23$, $P = 0.045$). In all the former analyses, no confounding factor (or their interactions) turned out to significantly affect any of the dependent variables (Tables 1, 2). Finally, food-handling bout duration of live animals did not vary between treatments ($\bar{X} \pm$ SE duration: no robot: 2.94 ± 0.42 s; immobile robots: 3.76 ± 0.41 s; robots with short head-up

Table 1. Foraging responses of live house finches to variations in the presence and behaviour of robots, taking into account the confounding effects of sex, temperature (temp.), weight at the beginning of the trial, and the time that animals were food deprived before the beginning of trials (food dep.). Results from general linear models

	Treatment (T)	Sex (S)	T×S	Temp.	Weight	Food dep.
Seed consumption, overall model, $F_{10,52}=3.64$, $P<0.001$, adjusted $R^2=0.30$						
F	9.57	1.27	2.28	1.65	1.31	0.29
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	<0.001	0.264	0.090	0.203	0.258	0.591
Partial Eta-squared	0.357	0.026	0.112	0.029	0.024	0.001
Proportion of time head-down*, overall model, $F_{10,52}=5.75$, $P<0.001$, adjusted $R^2=0.53$						
F	17.25	0.01	2.32	0.13	0.13	0.59
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	<0.001	0.992	0.086	0.724	0.719	0.447
Partial Eta-squared	0.500	0	0.128	0.001	0.002	0
Food search rate, overall model, $F_{10,52}=2.13$, $P=0.039$, adjusted $R^2=0.23$						
F	3.42	0.38	0.65	0.09	0.16	0.25
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	0.024	0.539	0.588	0.766	0.693	0.620
Partial Eta-squared	0.168	0.008	0.040	0.004	0.002	0.015
Food search bout duration, overall model, $F_{10,52}=2.68$, $P=0.010$, adjusted $R^2=0.21$						
F	4.56	1.27	1.45	1.10	0.09	0.82
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	0.007	0.265	0.239	0.299	0.768	0.370
Partial Eta-squared	0.216	0.023	0.082	0.014	0.004	0.034
Pecking rate, overall model, $F_{10,52}=2.39$, $P=0.020$, adjusted $R^2=0.19$						
F	6.64	0.89	1.20	0.08	0.07	1.14
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	<0.001	0.348	0.318	0.783	0.799	0.291
Partial Eta-squared	0.270	0.019	0.059	0.001	0.002	0.010
Handling food bout duration, overall model, $F_{10,52}=2.02$, $P=0.049$, adjusted $R^2=0.11$						
F	1.77	5.38	1.02	0.86	0.05	0.01
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	0.164	0.024	0.391	0.358	0.827	0.967
Partial Eta-squared	0.096	0.093	0.056	0.020	0	0.005

Significant P values are given in bold.

*Arcsine transformed.

bouts: 4.28 ± 0.40 s; robots with long head-up bouts: 3.88 ± 0.42 s). However, we found a difference between sexes (Table 1); live males had longer food-handling bout durations (4.19 ± 0.29 s) than did females (3.23 ± 0.28 s).

The overall proportion of time scanning varied significantly between treatments and between sexes, giving rise to interaction effects (Table 2, Fig. 4a). Taking into account the robot treatments, the proportion of time scanning decreased with the presence of robots ($F_{1,52} = 27.99$, $P < 0.001$), with robots moving ($F_{1,52} = 8.52$, $P < 0.005$) and with robots showing long head-up bouts ($F_{1,52} = 5.38$, $P = 0.024$). The interaction between treatment and sex was apparently the result of females showing a lower proportion of time scanning than males in the robots with long head-up bouts treatment ($F_{1,52} = 17.42$, $P < 0.001$), with no significant differences between sexes in the other treatments ($F_{1,52} = 0.01-1.47$, $P = 0.229-0.976$).

Scanning rate did not vary between treatments (Table 2, Fig. 4b), but we did find interaction effects between robot treatment and sex. This interaction stemmed from males scanning more often than did females in the no-robot treatment ($F_{1,52} = 4.04$, $P = 0.049$); the differences between sexes in the other treatments were not significant ($F_{1,52} = 0.07-3.64$, and $P = 0.062-0.785$). Finally, we found

no differences in scanning bout duration between robot treatments ($\bar{X} \pm SE$ duration: no robot: 21.51 ± 7.66 s; immobile robots: 15.98 ± 7.45 s; robots with short head-up bouts: 19.68 ± 7.38 s; robots with long head-up bouts: 16.86 ± 7.59 s).

Experiment with Conspecifics

The responses of house finches to changes in the behaviour of conspecifics were similar to those given to robots. Focal house finches increased the proportion of time spent head-down when the peripheral conspecifics tended to show long head-up bouts ($\bar{X} \pm SE$ proportion: long head-ups: 0.137 ± 0.019 ; short head-ups: 0.064 ± 0.015 ; GLM: $F_{1,10} = 6.61$, $P = 0.027$, partial eta-squared = 0.26). Body size ($F_{1,10} = 0.06$, $P = 0.666$) and ambient temperature ($F_{1,10} = 0.17$, $P = 0.687$) did not significantly affect head-down time. Focal birds also increased pecking rate when live peripheral conspecifics increased head-up bout duration (long head-ups: 2.27 ± 0.12 ; short head-ups: 1.91 ± 0.13 ; $F_{1,10} = 7.88$, $P = 0.019$, partial eta-squared = 0.33). Pecking rate was higher in individuals with higher body mass

Table 2. Scanning responses of live house finches to variations in the presence and behaviour of robots, taking into account the confounding effects of sex, temperature (temp.), weight at the beginning of the trial, and the time that animals were food deprived before the beginning of trials (food dep.). Results from general linear models

Treatment (T)	Sex (S)	T×S	Temp.	Weight	Food dep.	
Proportion of time scanning, overall model, $F_{10,52}=6.29$, $P<0.001$, adjusted $R^2=0.46$						
F	14.68	3.42	5.60	1.15	0.24	0.08
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	<0.001	0.070	0.002	0.287	0.624	0.778
Partial Eta-squared	0.461	0.064	0.241	0.017	0.006	0.001
Scan rate, overall model, $F_{10,52}=1.99$, $P=0.053$, adjusted $R^2=0.08$						
F	1.37	0.46	3.16	2.20	1.85	1.18
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	0.263	0.502	0.032	0.144	0.179	0.283
Partial Eta-squared	0.069	0.007	0.144	0.039	0.034	0.007
Scan bout duration, overall model, $F_{10,52}=1.67$, $P=0.113$, adjusted $R^2=0.02$						
F	0.12	0.44	0.87	0.28	2.10	0.01
df	3, 52	1, 52	3, 52	1, 52	1, 52	1, 52
P	0.950	0.511	0.460	0.601	0.153	0.922
Partial Eta-squared	0.001	0.033	0.009	0.005	0.084	0.003

Significant P values are given in bold.

($F_{1,10} = 6.47$, $P = 0.029$), but did not vary with ambient temperature ($F_{1,10} = 0.22$, $P = 0.652$).

DISCUSSION

Our results show that (1) adult house finches do react to the presence, motion and behaviour of models mimicking conspecifics in seminatural flocks, and (2) they invest more time in foraging and less in scanning, which leads to increasing seed intake, as the robots display long head-up bouts. These responses are compatible with the idea that house finches monitor the behaviour of conspecifics. We also corroborated that house finches respond to robots in similar ways to live conspecifics.

Different proximate behavioural mechanisms could be involved in the increase in food consumption. Time competition between scanning and foraging (Caraco 1979) probably caused animals to increase their monitoring of the surroundings without the presence of robots, which reduced food intake. This response reflects increasing levels of predation risks in solitary foraging conditions (Lima & Dill 1990; Roberts 1996; Lima 1998). When static robots were present, birds slightly increased the proportion of time invested in foraging-related activities (head-down), as well as the pecking rate. However, static robots did not cause a significant increase in seed consumption, probably because birds spent a considerable proportion of time monitoring the models without investing in foraging. Previous studies using static models (Krebs 1974; Drent & Swierstra 1977) assessed responses associated with the level of attraction to foraging patches based on the number and body postures of the models. Our results suggest that the sole presence of static models in different body postures might not be enough to evoke behavioural responses associated with decisions about patch exploitation in this species, and that the flow of social foraging information might be limited under these conditions.

The motion of robots mimicking different types of behaviours generated responses that are compatible with social information transmission in natural flocks. Fernández-Juricic & Kacelnik (2004) used European starlings, *Sturus vulgaris*, in similar experimental conditions: an artificial flock composed of three linearly placed and separated enclosures, with one bird in each. They found that birds in the centre of flocks were sensitive to variations in the behaviour (foraging or alert) of peripheral conspecifics at

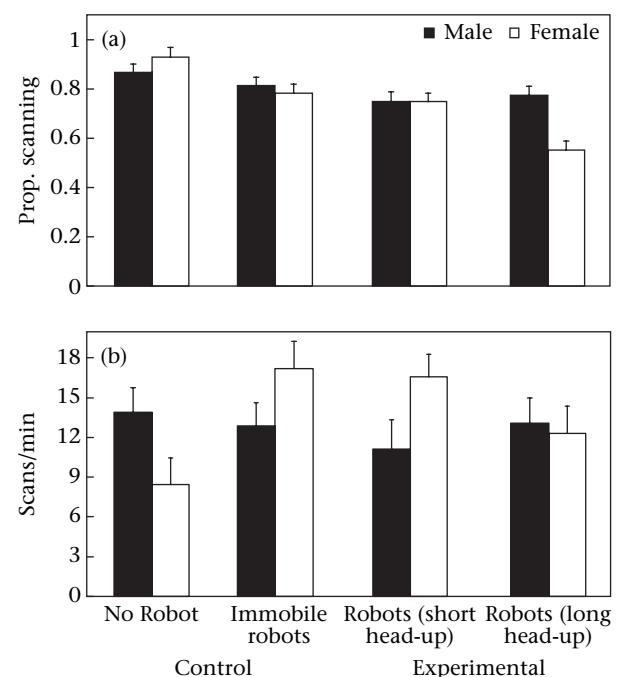


Figure 4. Scanning responses (a: proportion of time spent scanning; b: scanning rate) of male and female house finches to the presence and behaviour of robots, showing the interaction between treatments and sex. See Fig. 3 for treatment descriptions.

small neighbour distances. Starlings reacted by copying the behaviour of flockmates as the number of individuals performing the same kind of behaviour increased. In the present study, we manipulated two types of robot foraging behaviours instead, and found that house finches pecked more often and were more successful at consuming seeds when robots increased the length of head-up bouts after a head-down movement. This result could be interpreted as a successful foraging attempt (foraging with food handling), which in turn could increase the bird's attribution of value to its own patch (Valone 1993; Smith et al. 1999). This successful foraging stimulus was reinforced when the robots, after a long head-up, went back to head-down (pecking) behaviours. However, there are at least two alternative interpretations. First, an increase in handling time by the robots could be associated with higher scanning levels by the flock, which would reduce the costs associated with personal scanning and release more time for food searching (Pulliam et al. 1982; Lima 1995; Bahr & Bekoff 1999). This hypothesis is supported by a lower proportion of time scanning in the long head-up bout treatment. However, this decrease was affected by females reducing scanning time considerably (Fig. 2a), while males maintained scanning levels similar to the short head-up bout treatment. This result suggests that the prevalence of these two mechanisms could vary between sexes. A second interpretation is that house finch responses may be related to the ability of conspecifics to escape from predators. Cresswell et al. (2003) found that chaffinches, *Fringilla coelebs*, with short food search and handling times also detected predators more quickly. Thus, house finches may perceive robots with short head-up bouts as more efficient at avoiding predators, and they may decrease foraging effort to increase predator scanning and reduce risk.

We did not manipulate the foraging success of the robots after simulated pecking bouts (i.e. a robot actually chewing a seed), so the decisions of live house finches in this experiment were based on indirect information (the behaviour of the robots after head-down movements) rather than direct cues (the successful capture of a seed). Animals have been shown to pay more attention to direct cues than to the behaviour of conspecifics (reviewed in Giraldeau et al. 2002). However, when such cues are not available, conspecific decisions may become the only source of social information (Templeton & Giraldeau 1995). For instance, the ability of animals to use social information decreases with a slight increase in the distance between foragers (Fernández-Juricic et al. 2004b). In our experimental set-up, live house finches were separated by 1 m from robots, which could have increased the chances of using indirect information (e.g. robot behaviour) because of distance effects (Pöysä 1994; Proctor et al. 2003). Our results show that using indirect information from robots could lead to either correct or incorrect decisions (e.g. decreasing foraging investment despite high levels of food availability), which ultimately depends upon the initial foraging decisions of a few foragers (Giraldeau et al. 2002). This type of flow of information between group members has been defined as an informational cascade (Bikhchandani et al. 1992), which may help to explain patterns of ambiguous use of information, such

as flock-departure decisions during a predator attack (Lima 1994; Roberts 1997; Cresswell et al. 2000).

Our experiment adds new evidence to the responses of birds to robots reported in a previous study in social foraging contexts (Göth & Evans 2004), in that we assessed several foraging and scanning responses of adult birds of a social species, our experiment was conducted in environments in which animals usually forage, we evaluated the effects of the presence/absence of robots, and we tested for the effects of robot behaviours mimicking different foraging and scanning strategies. We conclude that robots have a great potential for advancing our understanding of the dynamics of social behaviour, and that some of their limitations can be overcome easily and may be a motivation to develop this technique further. For instance, animals may habituate to the repetitive motion patterns of robots. However, by making robot behavioural patterns more random, repetitiveness can be eliminated and habituation minimized. Thus, using robots will make researchers develop more precise and realistic models of animal behaviour repertoires, particularly for those species that are not very responsive to simple robot behavioural patterns. That level of mechanical sophistication, along with the use of skins and interactive robots, could allow researchers to assess how morphology (e.g. skin colour, texture) and behavioural patterns interact and vary in time to elicit different types of responses. Although developing robots as a new tool may be expensive, it may also create new funding opportunities for animal behaviour in the future.

This technique opens up new avenues to test certain hypotheses on the foraging and antipredator behaviour of flocks. Four examples follow. First, by manipulating the behaviour and position of robots in artificial flocks, some mechanisms of flock cohesion can be tested. One example of these mechanisms is the trade-off between neighbour distance, which may affect the ease with which a certain behaviour is perceived visually across the flock, and the behaviour of flockmates, which may modify the response of individuals (Fernández-Juricic & Kacelnik 2004). Thus, by varying the distance and number of robots, we could assess the contribution of social behaviour to explaining the group size effect and the threshold distance at which individuals become part of a flock. Second, the mechanisms of coordination of vigilance (e.g. taking turns scanning and foraging) have been thoroughly studied at the theoretical level (Ward 1985; Ruxton & Roberts 1999; Scannell et al. 2001; Rodríguez-Gironés & Vásquez 2002; Fernández-Juricic et al. 2004c), but empirical studies have been limited to observations of natural flocks (Bekoff 1995; Fernández-Juricic et al. 2003, 2004b). One alternative is to manipulate the body postures of large flocks of robots and observe the reaction of birds to determine the social and ecological conditions that would favour coordinated scanning as opposed to random scanning (reviewed in Bednekoff & Lima 1998). Third, given that under certain conditions some bird species, like the house finch, do react to indirect foraging cues, some of the mechanisms generating information cascades (e.g. responses to novel food items, flock departure decisions) can be studied by manipulating the behaviour of robots.

Finally, robots could be tools to assess the cues that animals use to gather social information in groups relative to foraging opportunities and predation risk, including types or frequency of conspecific body movements, head movements and food-handling behaviour. Identifying these cues would allow us to eventually study the transmission of social information in foraging groups.

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