

Persuasive companions can be wrong: the use of misleading social information in nutmeg mannikins

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Animals sample their surrounding environment to collect information, which can be obtained personally or by tracking the behavior of others (i.e., social information). Although social information appears to be generally advantageous, it can also be detrimental and may even conflict with personal information. We tested the effect that the strength of social information, and ultimately its persuasiveness, can have on an animal's decision to use it or not by conducting an experiment using single nutmeg mannikins (*Lonchura punctulata*), which were offered a foraging choice after observation of videos of feeding or nonfeeding conspecifics. The persuasiveness of social information was amplified by increasing the number and changing the behavior of conspecifics that had previously been seen feeding at 1 of 2 feeders. In addition, we modulated the certainty of an individual's personal information. Some birds had prior experience of a marked feeder always containing easily accessible food, whereas other birds experienced that this was only the case in half of the trials. Our results show that animals provided with sufficiently persuasive social information will tend to reduce the weight of even highly reliable personal information. This provides the first experimental evidence consistent with the propagation of informational cascades in nonhuman animals, which have been invoked to explain market crashes in economics or panic rushes in human crowds. *Key words*: informational cascades, *Lonchura punctulata*, nutmeg mannikins, personal information, social information. [*Behav Ecol*]

The quality or adaptiveness of an animal's behavioral decisions hinges on the accuracy of the information on which it is based (Stephens 1989). The type of information available to individuals will depend to some extent on their ecology. For instance, solitary animals will generally be limited to acquiring information directly from the successes and failures of their own decisions. In contrast, social animals can obtain information both by sampling the environment themselves and also by observing companions' decisions, using these as sources of social information concerning the value of different alternatives (Danchin et al. 2004).

It is generally assumed that because both asocial and social information are available to social animals, social individuals have access to more information when they must decide on a course of action. However, both sources of information may not be available concurrently, and individuals may need to decide on which source to use. There are 2 situations in which individuals may need to choose which source of information to use. In one case, limited attention (Dukas 1998; Fernandez-Juricic and Kacelnik 2004) may make it difficult to obtain both types of information concurrently, forcing individuals to decide whether to collect personal or social information. In the other, the 2 sources of information may provide conflicting results such that animals must decide which to use or how best to combine them (Laland and Williams 1998).

The ability of animals to modulate their use of social information adaptively has received growing attention (Kendal

et al. 2004; van Bergen et al. 2004). The degree to which animals will rely preferentially on social information appears to depend on the ease with which social and personal information can be simultaneously collected and the difficulty of gathering accurate personal information from the sampling of their environment (Templeton and Giraldeau 1995). When sampling the environment directly becomes time consuming and energy consuming, social information may provide the most efficient way to obtain detailed and reliable cues (Boulinier and Danchin 1997; Valone and Templeton 2002; Dall et al. 2005). Yet, empirical evidence from both birds and fish shows that when individuals can obtain accurate personal information easily and at low cost, they ignore social information and base their decisions only on their personal knowledge (Templeton and Giraldeau 1996; Templeton 1998; Day et al. 2001; van Bergen et al. 2004).

Although numerous studies have explored the circumstances under which animals balance their use of social information against the quality of their personal information, to date, no study has explored the possible effect that social information strength, and ultimately its persuasiveness, may have on an animal's decision to use it and possibly disregard its personal knowledge. The persuasiveness of social tutors is somewhat akin to quorum responses within groups that have recently been proposed as a possible mechanism to explain collective decision making both in humans and nonhumans. In this case, the propensity to exhibit a particular class of behaviors appears to be a function of the number of conspecifics performing it (Mallon et al. 2001; Seeley and Visscher 2004; Ward et al. 2008). An individual therefore could be more willing to conform to a group's decision when it sees some threshold number of group mates adopting this decision.

The persuasiveness of information emanating from social tutors has also been addressed by economists such as Bikhchandani et al. (1992, 1998). They have argued that under

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incomplete information optimal decision makers ought to make use of social information obtained by watching a sequence of others deciding before them. When animals do this, the information provided by a sequence of social tutors can induce herd-like phenomena or “informational cascades,” in which decisions are made in total disregard to the personal information at hand; individuals “blindly” copy the decision they witnessed in a sequence of others (Bikhchandani et al. 1998). Although copying predecessors’ actions often leads to the adoption of the correct decision, it is also prone to lead individuals into adopting incorrect decisions imposing fitness-related costs (Bikhchandani et al. 1998; Laland and Williams 1998; Giraldeau et al. 2002; Noth and Weber 2003). Such cascades are expected to occur when the observation of companions is limited to their decisions rather than the cues on which these decisions were based (Bikhchandani et al. 1998; Giraldeau et al. 2002).

Informational cascades have been argued to provide a coherent explanation for a number of large-scale explosive copying events such as market crashes in economics, panic rushes in crowds, as well as the accumulation of thousands of individuals at the same night roost, mate choice copying, and flock alarm flights (Giraldeau et al. 2002). However, if cascades really do explain such phenomena, it would first be necessary to demonstrate that individuals can disregard their own personal information when sufficiently persuasive contradictory social information is offered. Here we show that nutmeg mannikins (*Lonchura punctulata*), highly social nonaggressive estrildid finches (Giraldeau et al. 1990), can be induced to choose the wrong foraging patch when given sufficiently convincing but contradictory social information.

METHODS

Experimental subjects

We used 20 two-year-old unsexed adult nutmeg mannikins, all experimentally naive and selected randomly (here and thereafter using random number tables) from a colony of 35 birds purchased from a commercial supplier. All birds were individually identified by using a unique combination of colored leg bands. Birds were housed in groups of 4 in holding cages (38 × 53 × 30 cm; equipped with 3 perches, 3 feeders, 3 drinking through, a cuttlebone, and oyster shells) located in the Université du Québec à Montréal animal facilities and maintained on an ad libitum diet consisting of a mix of millet seeds. Water was always available, and lighting was set on a 12-h day:night cycle.

Recording videos of demonstrators

First, 12 birds were selected randomly from the 15 remaining birds of the colony to produce the video sequences to be played back during experimental trials. Birds were placed in a box (18 × 13 × 15 cm) made of 3 opaque and 1 transparent sides located in an observation room to record birds’ foraging behavior. The box was equipped with a feeder containing a mix of millet seeds. We recorded the video playbacks from the observation room using a remote controlled miniDV digital camera (Canon Optura 30) set on a tripod recording through a small peep hole in a black opaque curtain. To insure that videos presented life size animals, we controlled for depth cues on the screen by videotaping a feeder that only allowed birds to feed side-by-side facing the camera lens so that they all stood aligned in the same plane behind the feeder in front of the video camera. Therefore, all birds were taped at similar distances from the lens so that their playback image size was the same.

The birds were food deprived for 14 h (overnight + 2 h) as well as between 2 successive recording periods of the same day. We recorded the behavior of feeding groups 4 times per day at 90-min intervals during 4 days. After the last recording of the day, the birds were provided with an unlimited supply of mixed millet seeds until lights were turned off. We recorded video playbacks for all group sizes from 0 to 6 individuals. The identity of birds that made up each group size was selected randomly just before the birds were introduced to the apparatus. We edited the video sequences of feeding and nonfeeding groups of birds using Pinnacle Studio 9 software (Avid Technology Inc., Mountain View, CA). To control for pseudoreplication (McGregor 2000), we created four 6-min video sequences exemplars of each group size that were shown randomly during the experimental trials.

Apparatus

The apparatus consisted of a 90 × 50 × 30 cm box built from corrugated plastic divided into compartments A (25 × 50 × 30 cm) and B (65 × 50 × 30 cm; Figure 1). The experimenter (G.R.) would allow the bird to move from compartment A to B by remotely raising a mesh partition between the compartments. A TFT LCD video screen (Sony DSM-m61: resolution max: 1280 dots × 1024 lines, operating frequency 48–85 Hz, resolution > 600 lines) was used to play back video images of groups of birds. The video screen was placed just behind 2 feeders at the far side of compartment B. The video screen was positioned to play 2 video sequences simultaneously, one behind each food feeder. Although they were in compartment A and until they landed on one feeder, focal birds could not see the contents of the 2 feeders. Exposure to social information ceased when the video playbacks were stopped, the partition was then lifted and the focal bird was able to access compartment B and choose to eat at 1 of the 2 feeders. The 2 feeders were separated by an opaque barrier to prevent a bird from visiting both feeders during a trial. One feeder contained a large quantity of mixed millet seeds (a very palatable food for nutmeg mannikins) and so provided rapid feeding. The other contained a deep layer of nonedible dry peas covering a thin layer of millet seeds and so provided a slow laborious feeding opportunity because the birds had to search through the peas to gain access to millet. The locations of the fast and slow feeders were chosen randomly just before we introduced a focal bird into the apparatus.

Training and trials procedure

Focal birds were food deprived for 14 h (overnight + 2 h) as well as between 2 successive training and trial periods on the same day. Each focal bird was individually introduced to the experimental box 4 times a day at a 90-min interval during a 3-day period for a total of 12 trials per bird. We placed each bird in compartment A for 2 min before removing the mesh partition allowing them to access the feeders. Once the focal bird landed on one of the feeders, we considered the feeder as having been chosen. The bird was allowed to feed for 3 min before the experimenter gently removed it from the apparatus. During the training period, only video sequences of feeders without companions were played back behind the feeders.

Ten birds were trained individually in a situation where the fast feeder was always cued by a green dot on its side; thus, the dot was a strong predictor of the location of the fast feeder: the high personal information condition. Ten other birds were trained in a condition where the green dot was associated with the fast feeder in half the trials; thus, the dot failed to predict the position of the fast feeder: the no personal information

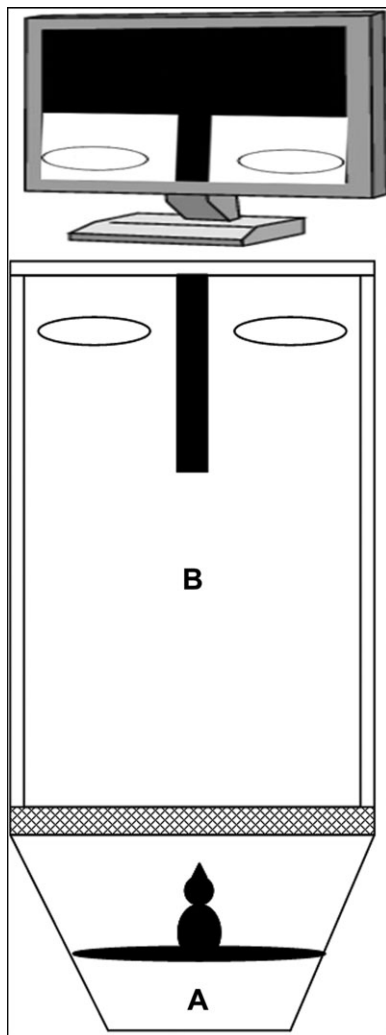


Figure 1

Schematic representation of the apparatus: each bird is individually introduced in the observation compartment A where it can observe the video sequences through the transparent partition. Once in compartment A, the focal bird cannot see the content of the feeders in compartment B, and once let into compartment B by remote raising of the partition between compartments A and B, it can choose its feeder using the visual cue on one of the feeders with which it had previous experience or/and the social information that had been provided by a video playback of companions behind one of the feeders.

condition. After this training period, the birds were given the opportunity to choose their feeder following exposure to a video playback that provided them with social information at 1 of the 2 feeders. To do this, we played a video sequence of companions behind one feeder, whereas a fixed image of a feeder with no bird was played behind the other. The quality of the social information was varied in 2 ways. We assumed that persuasiveness of social tutors was determined by both their behavior and their numbers. We assumed that social information was more persuasive when the birds in the playback fed from the feeder rather than merely standing on the feeder without any feeding. We also assumed that the persuasiveness of the social information increased with the number of birds seen in the playback. The social information could either coincide or not with the location of the green dot. Before each trial, the experimenter determined randomly the location of

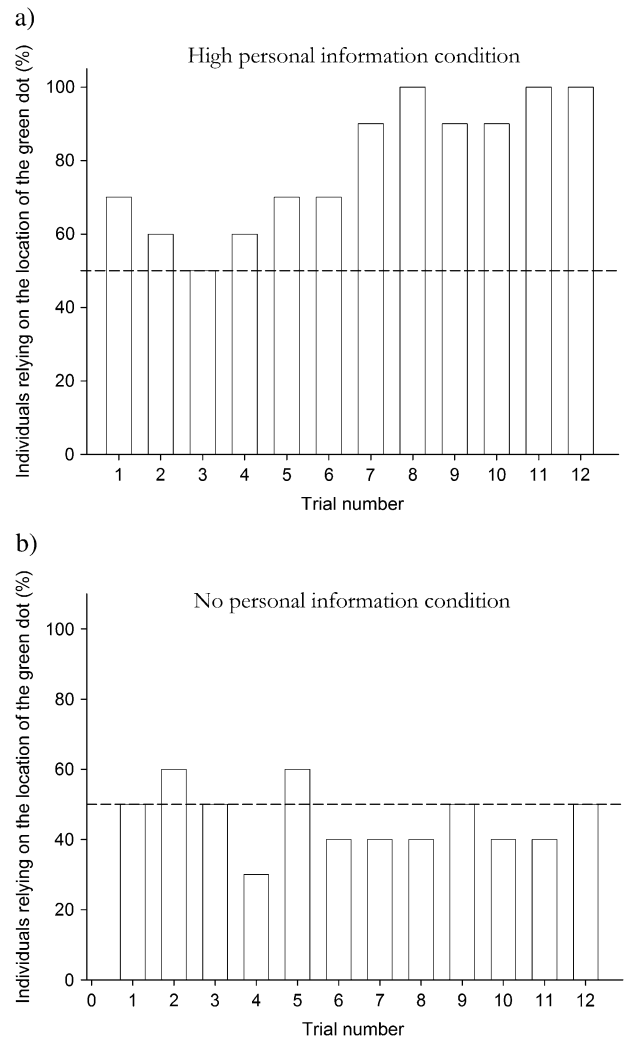


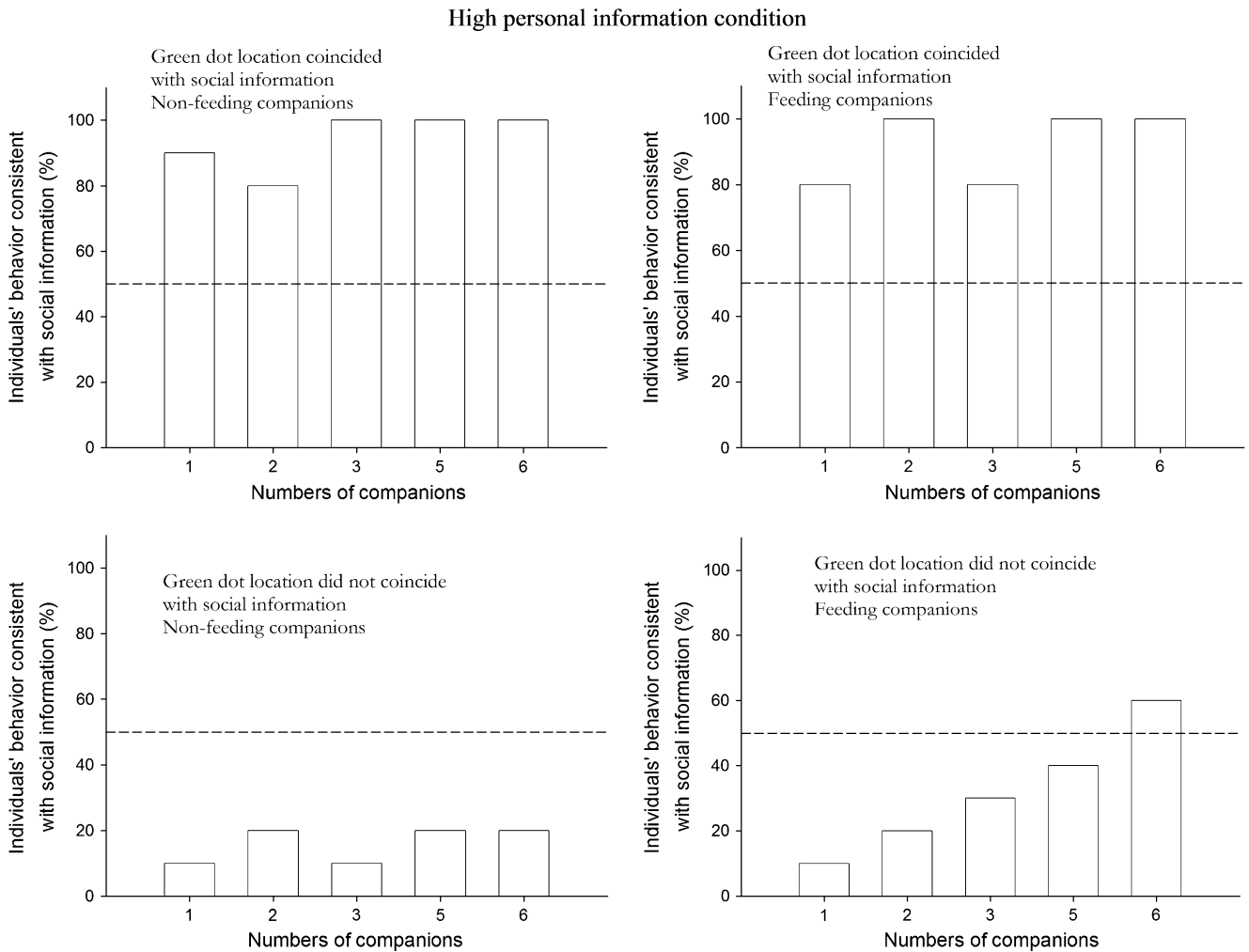
Figure 2

Proportion of focal birds relying on the green dot position to choose which feeder to exploit when previous training is such that the dot (a) predicts the location of the fast feeder ($N = 10$; high personal information condition) and (b) fails to predict the location of the fast feeder ($N = 10$; no personal information condition).

the fast feeder, the location of the green dot, the location of the social information, whether the companions would be seen feeding, and the size of the simulated group of companions (1–3 companions for the no personal information condition and 1–6 for the high personal information condition). We used a repeated measures design where each bird experienced each possible combination once (i.e., for each group size of feeding or nonfeeding companions and social information coincides or not with the position of the green dot). Birds were tested 4 times a day at a 90-min interval during a 6-day period in the high personal information condition (for a total of 24 trials per bird) and during a 3-day period in the no personal information condition (for a total of 12 trials per bird). We noted each bird's choice and allowed it to feed for 3 min before we reintroduced the bird to its holding cage. Throughout training and experimental trials period, no focal birds moved from their first choice feeder to the other.

Statistical analysis

We performed logistic regressions to investigate how focal nutmeg mannikins balanced their use of personal and social

**Figure 3**

Proportion of focal birds ($N = 10$) for which prior training was such that the green dot provided a strong predictor of the location of the fast feeder that relied on social information to choose their feeder, expressed according to the number and the behavior of virtual companions, and whether the social information coincided or not with the location of the green dot.

information. We built generalized linear mixed models with binomial distribution of errors, using the function `lmer` (package `lme4`) in R. The binary response of relying or not on social information was modeled as a function of personal information (green dot predictive or not of the location of the fast feeder), the persuasiveness of social information (the number and behavior of playback companions), and whether social information coincides not with the position of the green dot. As we used a repeated measures design, the birds' identity was included as a random effect in the generalized linear mixed models to control for the nonindependence of errors resulting from the repeated measurements on the same birds. We first fitted a global model (i.e., the most complex model involving all interactions) and evaluated models using Akaike's information criterion values (Akaike 1974) to select for the minimal adequate best-fit model. After that, data from only the high personal information and no personal information conditions were tested separately following the same model selection procedure.

RESULTS

Personal information trials

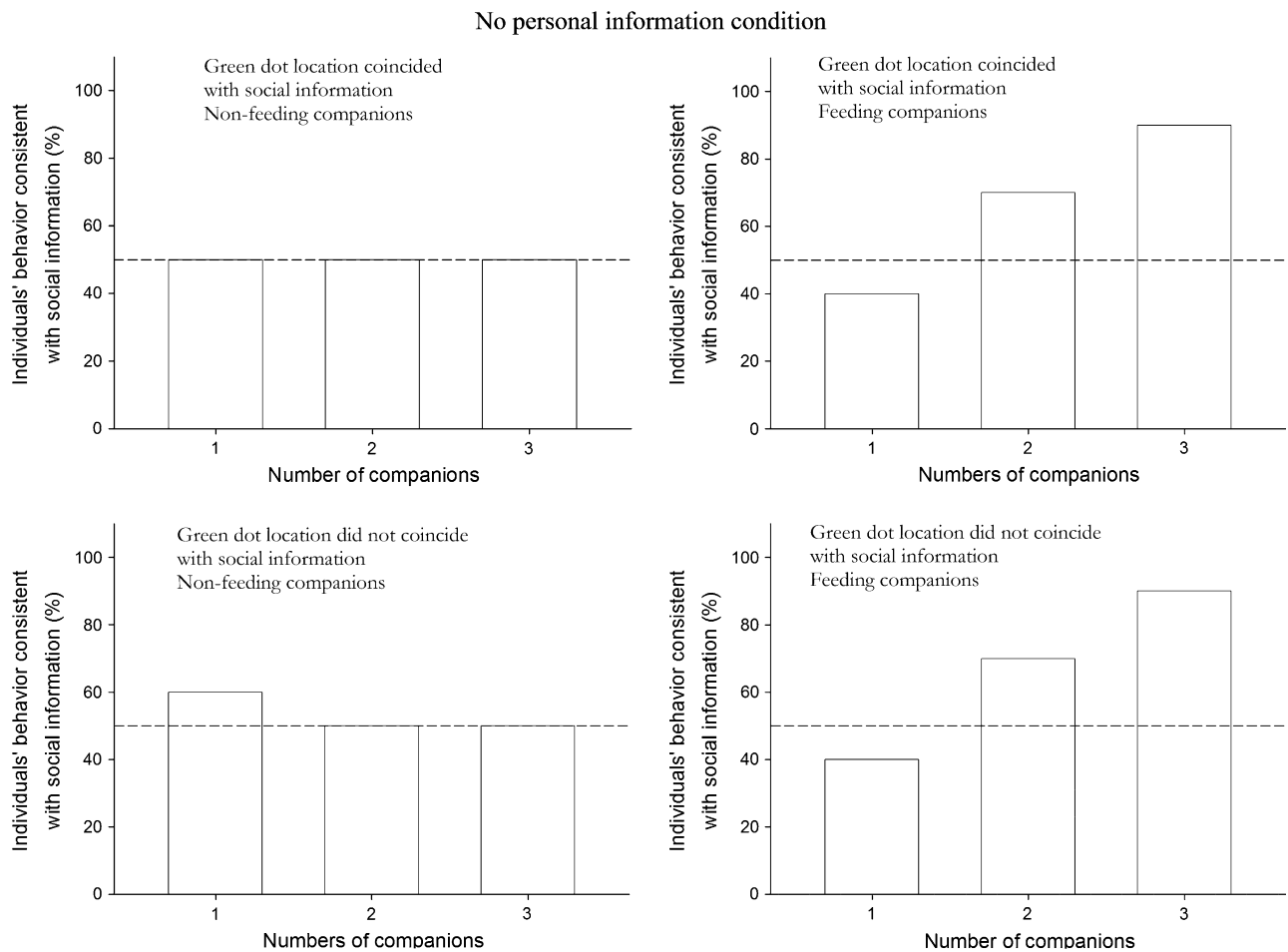
After 7 trials, 80% of the birds trained in the high personal information condition chose the feeder bearing the green dot

and so learned to rely on the dot to choose the best feeder. The proportion grew to 95% after 9 trials and remained at near that level through the last trial. The proportion of birds choosing the feeder bearing the green dot in the no personal information condition never exceeded 50% after the sixth trial, and so birds from this group did not rely on the green dot to choose a feeder (Figure 2).

Social information trials

The best-fit model ($N = 20$, degrees of freedom [df] = 8), for all data combined, retained the following predictors: the level of personal information ($z = -3.77$, $P < 0.001$), the number ($z = 3.77$, $P < 0.001$), and behavior ($z = 0.42$, $P = 0.67$) of companions, whether social information coincides or not with the position of the green dot ($z = -8.38$, $P < 0.001$), and the 2-way interactions between number and behavior of companions ($z = -2.05$, $P = 0.03$) and between personal information and whether social information coincides or not with the position of the green dot ($z = 6.94$, $P < 0.001$).

The predictors in the best-fit model for birds trained in the high personal information condition ($N = 10$, df = 5, between focal birds variance = 0.041) were the number ($z = 2.84$, $P = 0.004$) and behavior ($z = -1.65$, $P = 0.09$) of

**Figure 4**

Proportion of focal birds ($N = 10$) for which prior training was such that the dot failed to predict the location of the fast feeder that relied on social information to choose their feeder, expressed according to the number and the behavior of virtual companions, and whether the social information coincided or not with the location of the green dot.

playback companions and whether social information coincides or not with the position of the green dot ($z = -8.06$, $P < 0.001$). We retained the predictive variable of playback companions' behavior (feeding or not), although it did not reach conventional levels of statistical significance; the effect of playback companions' behavior on persuasiveness of social information appears weaker than the effect of companion number. However, when playback companions were observed to be feeding in the slow feeder, the number of birds that were observed to choose the slow feeder increased with increasing numbers of feeding playback companions (Figure 3).

The best-fit model for birds trained in the no personal information condition ($N = 10$, $df = 4$, between focal birds variance = 0.067) retained the number ($z = 2.05$, $P = 0.04$) and behavior ($z = -1.15$, $P = 0.24$) of companions. In this case, however, whether social information coincides or not with the position of the green dot was not retained as a remaining predictor of the best-fit model. This is because in the no personal information condition the green dot provided no information and so the social information could never contradict the personal information. The persuasiveness of social information for birds with no personal information increased with the number of companions (interaction between number and activity of companions: $z = -2.47$, $P = 0.01$; Figure 4).

DISCUSSION

We show here that birds that had prior experience with the green dot as a strong predictor of the location of the fast feeder could be induced nonetheless to ignore this information and choose nonetheless to feed from the feeder their prior experience identified as a slow feeder, after having seen a sufficient number of playback companions feeding at that feeder. Our results, therefore, provide experimental evidence that nutmeg mannikins will tend to disregard their personal information when social information is sufficiently convincing. Birds relied on social information more when the green dot failed to predict the location of the fast feeder.

It is not too surprising that birds with no personal information on feeder differences relied heavily on social information. Such a result confirms earlier findings obtained in fish (Kendal et al. 2004, 2005). However, the pattern that birds chose what they had learned to expect to be the slow feeder after having been exposed to persuasive social information provides the first experimental evidence within nonhuman animals that is consistent with the propagation of informational cascades observed in human crowds (Bikhchandani et al. 1998). The result shows that under some conditions socially acquired information can outweigh personal information. Obviously, it remains to be seen whether birds would continue to reduce the weight of their personal information after having

experienced that by following others they had chosen the wrong feeder. Our results, nonetheless, challenge the suggestion that high reliability of prior personal information can insulate individuals from the use of social information (Valone and Giraldeau 1993; Templeton and Giraldeau 1996; Templeton 1998).

Valone and Giraldeau (1993) found that when budgerigars (*Melopsittacus undulatus*) fed in groups they did not rely on social information but mostly used personal patch-sample information, combined with prior knowledge of food distribution to assess the quality of a currently exploited patch. Unlike budgies, nutmeg mannikins were able to combine prior knowledge about food location with information obtained from the observation of companions' behavior and number when deciding which feeder to exploit. Our study differs from the experiments involving budgies in that our apparatus prevented birds from collecting patch-sample information thus forcing them to rely exclusively on past personal and social information. Thus, our results suggest that when animals cannot collect information through patch sampling they will rely on social information about current conditions to decrease uncertainty.

The experimental setup provided a control for conspecific attraction given that no virtual birds were present during the choice phase. That conspecific attraction did not contribute to the subject's choice is highlighted by the pattern that we found that when virtual companions were not feeding, focal birds without any prior knowledge about food location were not influenced by the earlier exposure to companions. This adds support to the conclusion that birds relied on social information when they chose to forage at the patch where they had previously seen companions feeding. Learning socially can be efficient when it facilitates the diffusion of correct information at low cost within groups. But if it overrides personal information, it may also lead to the establishment of informational cascades that, once started, can prevent further accumulation of new information within the group. Informational cascades are more likely when personal information acquired by sampling remains ambiguous (Hirshleifer 1995; Bikhchandani et al. 1998). It would be unlikely for the high personal information birds to be tricked repeatedly by incorrect social information given that in our experiment personal sample information was quite unambiguous; once sampled, the feeder was unambiguously fast or slow. As a result, our situation is unlikely to produce a long lasting erroneous informational cascade. However, birds that had no prior knowledge of the existence of two discrete feeder qualities would be more prone to copy others and perhaps engage in informational cascades, some correct and some incorrect. We have shown that even birds with personal knowledge about the existence of discrete patch qualities can be induced to disregard this experience when provided with persuasive social information.

We should now turn to exploring the formation of informational cascades using naive individuals faced with the task of learning to associate a partially ambiguous cue signaling patch quality, when exposed to video playbacks of social companions that are already engaged in a cascade. We predict that learning in such a case would be difficult as the naive bird would be increasingly likely to join the cascade as the persuasiveness of the social information increases.

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