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Environmental Unpredictability and the Value of Social Information for Foraging Starlings

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Abstract

Environmental and behavioral cues are useful sources of information that allow group foraging individuals to improve their foraging success. Few studies to date, however, have examined how varying degrees of environmental unpredictability may affect when and how individuals use the social information they obtain in foraging groups. In this experiment, European starlings (*Sturnus vulgaris*) were tested to determine in which type of environment, predictable or unpredictable, social information would be the most valuable. Subjects were placed under one of four conditions: an unpredictable environment with either (1) an informing demonstrator bird or (2) an uninforming demonstrator; or a predictable environment with either (3) an informing demonstrator or (4) an uninforming demonstrator. Environmental predictability was manipulated by altering the meaning of available color cues. Subjects in the unpredictable environment that had an informing demonstrator performed significantly better than subjects in an unpredictable environment with an uninforming demonstrator, although only on the second day of testing. Subjects in both the predictable conditions performed similarly to each other. The results suggest that social information is more valuable to individuals in an unpredictable environment than it is in a predictable environment; however, there appears to be a time lag in the ability of the birds to recognize the value of this information.

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Introduction

Previous experiments on group foraging behavior have found that access to both personal and social information is important to individual foragers to increase their overall foraging success (reviewed by Krause & Ruxton 2002). Theoretically, individuals that are part of a larger foraging group can obtain valuable information about the quality of a foraging patch by watching the

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successes and failures of other members of the group and by making foraging decisions based on this information (Clark & Mangel 1984; Valone 1989). Empirical research involving different species of birds has found support for these theoretical models (Benkman 1988; Templeton & Giraldeau 1995b, 1996; Smith et al. 1999). For example, the success of a social forager, such as the European starling (*Sturnus vulgaris*), depends upon how quickly a bird can recognize the poor quality of a foraging area and depart to find another, more profitable area. Individuals can obtain this 'public' information (Valone 1989) through vicarious sampling, which allows them to forage more efficiently than they would as solitary foragers (Templeton & Giraldeau 1996). Group foragers can also pay attention to environmental cues produced by the foraging activities of their companions, and use these cues to influence their scrounging decisions (Templeton & Giraldeau 1995a) and to detect (Krebs 1973; Palameta 1989) or avoid (Mason 1988; Templeton 1998) foraging sites or prey types.

Two different approaches can be taken to study how animals use social information. The first is a psychological perspective, which focuses on the mechanisms of social information use, such as local enhancement (Thorpe 1963; Palameta & Lefebvre 1985), in which individuals are attracted to the area of successful foragers, and stimulus enhancement (Palameta & Lefebvre 1985; Galef 1988), where foragers pay attention to the cues associated with foraging success. The other perspective is an ecological one, which is more concerned with the types of environmental conditions that might favor social information use (Benkman 1988; Lefebvre & Palameta 1988; Dolman et al. 1996) and how this social information can influence foraging success. In this study, we take a psychological approach to answer the following ecological questions about social information use: what environmental conditions favor the use of social information by starlings, and when is this social information most valuable?

The value of social information may be defined as the difference in intake rate and foraging success between individuals that have relevant social information available to them and those that do not (Stephens & Krebs 1986). Templeton & Giraldeau (1996) found that starlings acquired and used social information only when they found it more costly to rely solely upon their own individual sampling information to assess the foraging patch quality. These results suggest that the value of social information may vary depending upon the type of foraging environment that is present. Thus, in an environment where the location of food is predictably associated with consistent contextual cues, the value of social information will be less than that in an environment where such cues are unpredictable (Stephens 1989). Boyd & Richerson (1988) made a similar prediction in their evolutionary model of social learning. This model showed that when it is costly to acquire accurate information individually, the use of social information should increase.

In a preliminary attempt to examine how environmental predictability affects the value of social information, we carried out a group foraging experiment with captive starlings. Our experiment consisted of four different environmental treatments. The treatments differed both in the predictability of foraging cues and the type of social information available: (1) predictable/informing (PI), in which the subject observed a conspecific ('demonstrator') foraging in a predictable environment where one cue was consistently associated with a reward; (2) predictable/uninforming (PU), in which the environment was again predictable, but the foraging demonstrator provided irrelevant social information to the observer about environmental cues; (3) unpredictable/informing (UI), in which the cue that was associated with reward changed from trial to trial, but the demonstrator always indicated the pertinent cue; and (4) unpredictable/uninforming (UU), in which subjects were in the same environment as UI, but did not receive any relevant social information from the demonstrator.

We hypothesized that social information would be more valuable in an unpredictable environment, and predicted that subjects would be much more likely to rely on social information in the unpredictable treatments than in the predictable treatments. Thus, we expected that the difference in foraging performance between subjects with or without relevant social information would be greater in the unpredictable environment than in the predictable environment.

Methods

Subjects and Apparatus

We used 22 wild-caught, adult starlings, 20 as naïve subjects (observers) and two (one male and one female) as demonstrators. We randomly assigned each of the 20 naïve subjects to one of four treatment groups ($n = 5$ birds per group), in which the first term refers to the type of environment and the second term refers to the information provided by the demonstrator: (1) PI, (2) PU, (3) UI, and (4) UU. Each demonstrator was used in all four treatments. All birds were maintained on a 12.00:12.00 hours light:dark cycle in individual home cages measuring 44 × 44 × 55 cm. The birds were held together in one room, and were provided with water and fed on a diet of breadcrumbs, insectivorous mix, turkey starter crumbs, and fruit pellets. Birds were maintained on a deprivation schedule to establish a testing weight of 85–90% of their ad libitum body mass during training and testing periods. After testing, each bird received ad libitum feeding for at least 3 d prior to release at point of capture.

For all experimental trials, we placed one subject in a test cage (60 × 45 × 45 cm) that adjoined another test cage of the same size, which held the demonstrator. Both cages had a sliding floor tray, which was used to slide the discrimination apparatus in and out of the cage. The test apparatus used for the demonstrator was a wooden block (55 × 10 × 2 cm) with three wells (2.5 cm diameter) drilled into it 5-cm apart. Circles (5 cm diameter) printed on white paper were placed over the wells during trials. Depending on the treatment group (see below), these three circles were either all white, or were different colors or patterns. The color combinations presented to each treatment were red, green, and yellow (two birds), or were pink, tan, and blue (one bird). The black, white, and gray patterns (two birds) consisted of a white star on a gray background, a gray triangle on a white background, and black squares on a white background.

We switched to patterns because some of the birds developed color biases or aversions, which are described in the results. The subject's testing apparatus consisted of three separate wooden blocks measuring 8.5 × 8.5 × 2 cm; each with a single 2-cm-deep hole drilled into it and covered with a single circle (5 cm diameter) printed on white paper. Each circle was of a different color or pattern, as described above. Prior to the experiment, demonstrators and subjects were first trained to retrieve a mealworm reward from a single wooden block by piercing through a piece of white paper over the well.

Procedure

Each subject received 10 test trials a day for 3 d. A test trial consisted of one demonstration performed by the demonstrator followed by a choice performed by the subject. The apparatus was presented to the demonstrator in the sliding tray, on the side of its cage adjacent to the subject's cage (Fig. 1). Only one of the three circles concealed a mealworm reward. The position of the rewarded hole was chosen randomly, with the constraints that each hole was rewarded an equal number of times across the 3 d, and that no hole position was rewarded two times in a row. In the unpredictable trials, each color was rewarded an equal number of times across the trials and never consecutively. In the predictable trials, the same color was rewarded each time, but the position was still randomly chosen. The demonstrator had to pierce all three of the holes even after the reward was found so that both successful and unsuccessful information was available to the subjects;

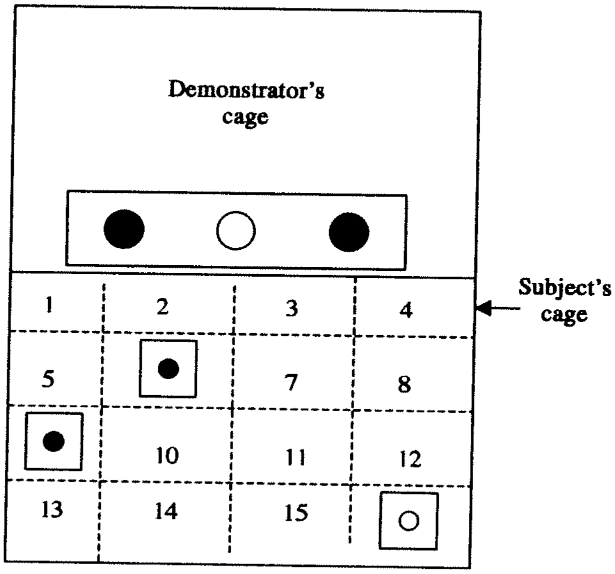

Fig. 1: Top view of experimental set-up of cages and apparatus for demonstrator and subject

starlings are known to use both types of information (Templeton & Giraldeau 1996; Templeton 1998). The demonstrators were willing to keep searching even after they had found food because they performed for subjects in all four conditions; thus, they associated several colors with reward. In addition, their initial training trials often had food in more than one hole, so the deprived demonstrators were motivated to search for food in all three holes. The subject was given a choice test immediately following the demonstration of the task. The three choice blocks were positioned randomly on a grid of 16 squares drawn on the subject's sliding tray (Fig. 1). Squares 1–4 were never chosen because of their proximity to the demonstrator. During a choice trial, the subject was only allowed to pierce one hole. All three blocks were then removed, and the apparatus was prepared for the next trial. The inter-trial interval was 2 min.

Experimental Design

In both of the predictable treatments (PI and PU) the rewarded cue remained constant across all 3 d of testing, but the position of the mealworm reward changed for both the demonstrator and the observer. In both of the unpredictable treatments (UI and UU) the rewarded cue changed from trial to trial and over testing days; the position of the mealworm reward changed as well. In the informing treatments (PI and UI) the demonstrator and the observer were each presented with the same combination of three colored or patterned circles and the observer had the same rewarded cue as the demonstrator. In the uninforming treatment groups (PU and UU), the demonstrator was given three white circles (irrelevant information), whereas the observer was presented with the same three colored or patterned circles on every trial. We alternated treatments throughout the experiment.

All trials were observed from behind a blind on a television screen connected to a camcorder (Handycam, Sony, Japan). We measured the daily performance of each bird as the number of correct responses in 10 trials. A two-way repeated measures analysis of variance (RM-ANOVA) was used to analyze data for a day effect, environment effect, information effect, and all interaction effects. Tukey's post hoc tests were used to determine the cause of the interaction effect. Data were analyzed with SYSTAT (Wilkinson 1990) and Microsoft Excel.

Results

Each observer in each of the four conditions completed 30 trials over the course of 3 d (Fig. 2). There was a highly significant effect of the environment on performance ($F_{1,16} = 190.311$, $p < 0.001$), with the birds performing significantly better overall in the predictable conditions than they did in the unpredictable conditions (Fig. 2). There was also a significant day × environment interaction ($F_{2,32} = 20.528$, $p < 0.001$), which reflected the greater improvement in foraging success in the predictable environments than in the unpredictable environments. However, there were no significant interactions between day and information

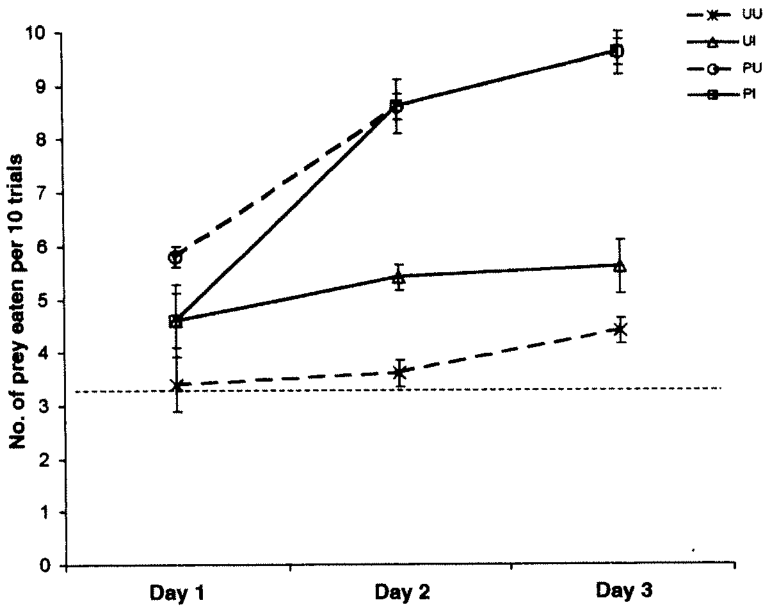

Fig. 2: Mean performance of the four environment/information treatment groups over three days of testing. UU = unpredictable/uninformed, UI = unpredictable/informed, PU = predictable/uninformed, PI = predictable/informed

($F_{2,32} = 1.279$, $p < 0.292$), and the three-way interaction term was not significant either ($F_{2,32} = 0.548$, $p < 0.583$).

There was no significant effect of information type on foraging success, although there was a trend ($F_{1,16} = 4.369$, $p = 0.053$). Most noteably, however, there was a significant interaction between environment and information ($F_{1,16} = 14.155$, $p = 0.002$). This interaction effect resulted from the fact that there was a significant difference in foraging success between UU and UI on day 2 (Tukey's post hoc test, $p = 0.007$), but not on day 1 ($p = 0.365$) or on day 3 ($p = 0.137$). Thus, the social information provided to the subjects in the unpredictable environment played a role in their improvement (Fig. 2). However, although the UI birds improved in their performance on day 2, the difference between UI and UU birds on this day was also due to the decreased variance in the birds' performance. This decreased variance may have been due both to a delay in the time it took for the UI birds to start paying attention to the demonstrator's information, and to color biases exhibited by the UU birds (see below). A color bias would have kept performance consistently at random because a particular color was only rewarded a third of the time. There was no significant difference between PI and PU on any day, which confirms that the significant interaction effect resulted only from the difference between UU and UI on day 2. The mean difference in foraging success between UU and UI conditions on this day (1.8 worms) represents the value of the social information. It is combination of these two species' characteristics. On the one hand, starlings are highly gregarious, with plenty of opportunities to acquire social information; and on the other, they are also highly exploratory, which suggests they must rely heavily on their own information to learn about different foraging environments.

In predictable environments, the birds with access to social information (PI) did not necessarily need to use it to be successful in that environment. Although both personal and social information were available to these birds, there were no significant differences in foraging success between PI and PU conditions. Starlings have been found to ignore social information when it is not easily available to them or when accurate personal information can be obtained at low cost (Templeton & Giraldeau 1996). The overall improvement in foraging success from day to day in both predictable conditions suggests that starlings learned individually which cue was associated with the food reward. These findings are consistent with other studies that used color and pattern cues associated with a food reward (Draulins 1987; Palameta 1989; Templeton 1998).

To consider, further, how valuable social information is to individuals in an unpredictable environment, it is necessary to discuss what types of inappropriate or unusual behaviors might result when there is a lack of reliable information (personal or social), especially about the presence of food. For example, only starlings in the UU condition developed both color aversions and color biases during the test trials. Most likely, birds formed these biases because the unpredictability of the environment prevented them from acquiring accurate information about the location of food. It is possible that UU birds picked one color cue on which to focus in an attempt to forage systematically in the unpredictable environment. Other studies have found that birds, particularly in captive settings, start to exhibit inappropriate behaviors, such as the development of color biases and position biases, when no other source of information is available (Templeton 1998; Templeton et al. 1999). In contrast, there were no significant pattern or position biases in UU birds; thus, it appears that this type of cue is more appropriate for foraging experiments (e.g. Draulins 1987).

Conclusions

We have shown that the foraging success of starlings is affected both by the environment in which they are foraging and by the availability of social information. Our results suggest that social information about the environment, specifically the association between environmental cues and the presence of food, is more valuable to individuals when they are in an environment that is unpredictable. However, it appears that these starlings required more extensive experience with the unpredictable environment before they would be willing to use social information preferentially over their own personal information.

It is important to address how realistic this study is and whether it can be applied to starlings in natural populations. It is true that the cues used in this study were artificial, and we did exaggerate the unpredictability of the experimental environment, but this factor is balanced out by the characteristics of starlings as a species. Starlings are an opportunistic, generalist species; they are equally at home in man-made and natural habitats (Cabe 1993). Within their lifetimes they will probably encounter new and different environments, in which they will most likely need to use social information that is available to them to enhance their foraging success (Lefebvre & Palameta 1988).

In future studies, it would be beneficial to investigate how different degrees of environmental predictability affect the frequency with which starlings make foraging decisions based on socially acquired information vs. personal information. It would also be helpful to avoid color cues altogether to avoid the potential development of color biases, and to use only pattern cues instead. In our study, however, the fact that color biases occurred only in those birds lacking sufficient foraging information reinforced the suggestion that the value of social information is higher in an unpredictable environment than it is in a predictable one.

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