COMMENTARY

Eurasian jays predict the food preferences of their mates

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The cognitive abilities of animals continue to fascinate both scientists and nonscientists. Although the abilities of the primates, our closest living relatives, generally attract most interest, several different lines of research have demonstrated high levels of intellectual capacity in birds, particularly corvids. The members of this family are known for their large brains and have performed well in many cognitive tasks using different paradigms (1–3). This finding has led to substantial revision of thinking about avian intelligence, including the suggestion of convergence in the evolution of cognitive abilities between corvids and primates (4). In PNAS, Ostojić et al. (5) add significantly to this literature with a very elegant experiment demonstrating the ability of male European jays (*Garrulus glandarius*) to predict the feeding preferences of their mates. The study is significant for many reasons: it demonstrates a high and unexpected level of flexibility, reports results bearing strong resemblance to human state-attribution and further confirms the importance of studying cooperative as well as competitive situations.

The Experiment

Ostojić et al. (5) take advantage of natural courtship feeding during which a male selects food to feed his mate, raising the possibility that his choices reflect the male's estimate of the female's motivational state. This approach is especially interesting because female preferences change with experience, thus requiring the male to track changes in his mate's preferences. A phenomenon known as "the specific satiety effect" allowed development of a method to manipulate female preferences.

In cases of specific satiety, recent experience eating a specific food induces a reduction in the attractiveness of that food, an effect that occurs in animals (6) and humans (7). In their first experiment, Ostojić et al. (5) determined whether European jays show specific satiety effects (figure 1*A* of ref. 5). The results show that prefeeding on either wax worm (W) or mealworm (M) larvae, presented separately in different sessions, induced specific satiety. In every case, females chose more W than M after prefeeding M, and more M than W after prefeeding W (bottom two rows of table 1 in ref. 5). This result is particularly impressive given that many of the females had clear preferences, some for W and some for M, after prefeeding on the maintenance diet (MD). The next experiment tested to determine if males adjust their behavior according to specific satiety after seeing their mate eat either M or W.

This second experiment had six sets of trials per mated pair, each with a prefeeding stage and then a test stage (figure 1*B* of ref. 5). During three of these sets, males were first allowed to watch their mates feed on MD, M, or W, and then given the opportunity to choose between M and W to feed to their mates. The other three sets were identical except that an opaque screen ensured the male could not see his mate eat during prefeeding. This design includes two notable features. The unseen condition provides a critical control for the effects of female behavior during the test itself, a type of control too often omitted (8). The inclusion of the MD prefeeding condition provides a critical baseline measure that allows statistical isolation of variance because of the large individual differences among the jays. With this design, the devaluing of a prefed food (W or M) needs to be measured against "... a baseline in which the food was not devalued ...." (5). When this comparison is made, the data are in accord with the specific satiety hypothesis: a male that saw his mate feeding on M, for example, preferred to feed W to his mate compared with feeding W to his mate following baseline MD prefeeding.

A third experiment (figure 1*C* of ref. 5) tested another alternative, that male food preferences themselves were affected by seeing what the female ate during prefeeding. If observing his mate feed on food W, for example, induced a reduced male preference for W, this preference could govern the male's choice of what to feed his mate. However, when males watched their mate eat M or W, this had no effect on the male's subsequent food choices when choosing food to eat himself. This finding supports the specific satiety hypothesis and demonstrates that self-feeding and courtship feeding are distinct.

The Interpretation and Significance

Overall, the results of these experiments, summarized in Ostojić et al.'s (5) figure 3 are consistent with the claim of state attribution. Male choice during courtship feeding anticipated the preferences of the female as if the male had knowledge of specific satiety. This result cannot be taken for granted; there are hypotheses that make different predictions. For example, animals sometimes copy the food choices of others (9), and seeing another animal choosing to eat a specific food could be taken as an expression of the current food preferences of that individual, thus predicting behavior opposite to specific satiety. This "copying" effect, although in the opposite direction to specific satiety, could still be taken as consistent with state attribution, but with a different rubric: if the female is choosing to eat it, she must like it. It would be interesting to learn if observing females freely choose food would produce different effects on male courtship feeding than those produced by feeding with just a single food present.

It must be noted that the alternative prediction of the copying hypothesis makes the use of one-tail statistical tests by Ostojić et al. (5) problematic because results opposite to their predictions would be meaningful. One should not, however, reject their conclusions. Much to the credit of the authors and PNAS, the individual data from all three experiments are presented in table 1

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of ref. 5. I suggest those with doubts about the statistical status of the findings explore these data with their own analyses before rejecting the conclusion that there is a specific satiety effect. For one thing, decisions about research outcomes should rest on more than a single data analysis or statistic (10). This process led me to conclude that interpreting the results as support for the specific satiety hypothesis is reasonable.

Ostojić et al. (5) highlight two salient facts: (*i*) the males actually had to see what the female ate to predict her specific satiety, and (*ii*) they did not simply match either her preferences or their own. These facts, the authors argue, offer evidence that male European jays may be capable of "…ascribing desire to their mates." The authors further argue that their results suggest the jays are capable of self-other differentiation, and also draw parallels between their data and data from studies of human motivation. However, what exactly does the specific satiety effect mean in terms of what males know about the motivational state of their mates?

This difficulty is the result of a general problem for students of animal cognition: judging the complexity of the cognitive structures underlying complex behavior. This problem was recognized by Charles Darwin in *The Descent of Man* when he pointed out that it is difficult to distinguish the behavior of man and higher animals, which is "..... founded on the memory of past events, on foresight, reason and imagination, with exactly similar actions instinctively performed by the lower animals; in this latter case, the capacity of performing such actions having been gained, step by step, through the variability of the mental organs and natural selection, without any conscious intelligence on the part of the animal during each successive generation" (11). Foresight and reason are not the only means of solving complex problems. (Darwin might well be delighted to learn that he had underestimated the level of cognitive functioning in the "lower" animals, which presumably would have included birds.) Careful research is needed to distinguish among possible cognitive mechanisms. Although some may doubt the ability to empirically determine the role of cognitive structures, such as state attribution in animals, there should be general agreement for the need for more research following up the results of Ostojić et al. (5).

There are several distinct and interesting questions about specific satiety and courtship feeding that arise. For example, Ostojić et al. (5) argue that the connection between the female's prefeeding and subsequent courtship feeding is not likely to have been learned by the male. There may, however, be specific experiences that are necessary for the male to be able to modify his courtship feeding as a result of observing his mate's behavior. Does modification require, for example, experience with rejection of food by the mate? According to Table 1 in ref. 5, there were many trials during which the female obtained no food from the male. Were many of these a result of the female rejecting the male's offering? Ostojić et al. (5) also argue that the male's choices were independent of the male's own desire-state/specific satiety, as indicated by the results of their third experiment in which there were no effects of the female prefeeding on different foods on the male's later choice of food for his own consumption. Further exploration of this issue would be desirable. For example, the food prefed to the males could be systematically varied to see if this had any influence on food chosen for courtship feeding.

There are two major contemporary approaches to studying animal cognition. One approach emphasizes using naturalistic contexts in which behavior is relatively unconstrained [e.g., caching behavior (1), tool use (12), or competitive interactions (3)]. The interpretation of many of these experiments emphasizes mentalist concepts, such as state-attribution or "theory of mind." The other approach has a history rooted in behaviorism and experimental psychology. This approach emphasizes laboratory studies, rigorous controls, and mechanist explanations, and the experimental settings usually severely constrain the behaviors available to the animals being studied (e.g., in operant chambers).

Although these approaches may seem incompatible, they can be complementary in many respects. More synthetic research combining the best features of each approach would be of particular value because the approaches complement each other. Naturalistic studies are usually particularly strong in having clear biological/adaptive relevance and connection to the lives of the animals in nature. However, it is often difficult when working with naturalistic methods to exercise precise experimental control over important variables, such as the exact sequence or timing of critical events. In contrast, laboratory studies can make precise control practical, allowing a greater range of tests of competing hypotheses about cognitive mechanisms. However, it is often difficult to identify the biological/adaptive relevance of the experimental setting. Although there are many examples integrating these approaches (e.g., refs. 13 and 14), much more effort along these lines is needed. Indeed, one of the reasons that the Ostojić et al. (5) experiment is notable is for their use of techniques, such as standardizing motivation through consistent feeding regimens before sessions and controlling female feeding by offering only one food to the female during each prefeeding. Although their interpretation in terms of the possibility that European jays ascribe internal states to other jays may be controversial, their data demonstrate an impressive degree of behavioral flexibility and should encourage others to vigorously pursue the nature of the cognitive abilities their results reveal.

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