Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays

Ljerka Ostojić, Rachael C. Shaw, Lucy G. Cheke, and Nicola S. Clayton[1]

Department of Psychology, University of Cambridge, Cambridge CB2 3EB, United Kingdom

State-attribution is the ability to ascribe to others an internal life like one's own and to understand that internal, psychological states such as desire, hope, belief, and knowledge underlie others' actions. Despite extensive research, comparative studies struggle to adequately integrate key factors of state-attribution that have been identified by evolutionary and developmental psychology as well as research on empathy. Here, we develop a behavioral paradigm to address these issues and investigate whether male Eurasian jays respond to the changing desire-state of their female partners when sharing food. We demonstrate that males feed their mates flexibly according to the female's current food preference. Critically, we show that the males need to see what the female has previously eaten to know what food she will currently want. Consequently, the males' sharing pattern was not simply a response to their mate's behavior indicating her preference as to what he should share, nor was it a response to the males' own desire-state. Our results raise the possibility that these birds may be capable of ascribing desire to their mates.

corvid | Theory of Mind | cooperation | specific satiety

In human development, the earliest manifestation of state-attribution is the ability to explain and predict others' behavior in terms of desire-states (e.g., wants, wishes, hopes), a capacity that does not require a concept of others' mental representations (1, 2). At around the age of four, the more complex desire-belief system is formed by incorporating the attribution of epistemic mental states (e.g., belief, knowledge, doubt, expectation) (3, 4), an ability known as Theory of Mind. It is very possible that the attribution of desire-states may represent not only the developmental, but also the evolutionary, precursor of Theory of Mind. Thus, the first logical step in the investigation of state-attribution in nonhuman animals should be to search for this simpler manifestation (5). Despite this, most comparative studies focus solely on the attribution of epistemic mental states (6–13).

A notable exception claims that apes can retrospectively infer humans' desires toward food items from the emotions expressed (14). However, given that the apes were explicitly trained about the relationship between human expressions and the availability of food, we cannot conclude that the apes inferred an underlying desire. In another study, the authors claimed that capuchin monkeys *(Cebus apella)* attribute a need or desire to another individual and thus might exhibit empathetic perspective-taking because the number of tolerated thefts by another individual was lower after subjects had seen the other individual eat than when they had not (15). Unfortunately, this study failed to account for a much simpler competitive account, namely that the sight of another monkey eating triggered the monkeys to protect their food. A second issue is that this experimental paradigm could only investigate the understanding of another individual's physiological processes, thus precluding an interpretation involving state-attribution, regardless of the results. Although physiological states such as hunger are used in reasoning about others' behaviors, they are not considered an internal, psychological state like desires and beliefs because the former lack the defining criterion of being "about something" (2).

In the present study, we investigated whether male Eurasian jays could attribute changes in an internal desire-state to their female partner. Desire-states can be manipulated by satiating individuals on a given food, leading to a decrease in their preference for eating that food, a phenomenon termed specific satiety (16–18). Specific satiety is specific because it reduces the desire for one food without necessarily impacting upon the desire for other foods. To illustrate; imagine that I usually buy myself a sandwich and a cake for lunch, but today I ate a sandwich immediately before lunch. This will not mean that I will now buy two cakes, merely that I will not buy the sandwich.

Results

In the present study, we induced specific satiety by prefeeding birds on either wax moth larvae (W) or mealworm larvae (M) and subsequently giving them the choice between these foods (the specific satiety experiment, Fig. 1A; see *Materials and Methods* for a description of the procedures). Because there was a large degree of interindividual variation in the amount of food eaten and in the individual birds' preferences for one food over the other, it was crucial to compare the birds' choices in these test trials with their eating pattern in a baseline in which birds were prefed maintenance diet (MD). All 13 Eurasian jays developed specific satiety; the proportion of W eaten relative to the baseline (prefed MD) was lower after birds had been prefed W than after they had been prefed M (Fig. 2, exact Wilcoxon signed-rank test, $n = 13$, $T = 0$, $P_{one-tailed} < 0.01$; Tables 1 and 2). Additionally, there was no difference between the sexes (exact Mann–Whitney U test, $n_{males} = 7$, $n_{females} = 6$, $U = 9$, $P_{two-tailed} > 0.05$). The specific satiety procedure thus provided an appropriate paradigm with which to manipulate the desire-states of the females.

To investigate whether male Eurasian jays respond to changes in their mates' desire-state (as induced by specific satiety), we used the highly cooperative courtship behavior of food sharing in which the male actively gives food to his mate. A fundamental feature of human state-attribution is its hypothesized evolutionary link with cooperative behaviors (19–21). Although the importance of a cooperative context has been addressed in research on empathy (22, 23), the majority of studies on state-attribution in nonhuman animals have used competitive paradigms (6–12). This focus emphasizes that nonhuman cognition might be better adapted for competitive than for cooperative contexts (24) and yet neglects the true nature of state-attribution as we understand it (25). Food sharing provides a unique means of assessing state-attribution in nonhuman animals within a cooperative context.

A male that takes his mate's specific satiety into account should adjust his food-sharing behavior after observing her being prefed on a particular food and share less of that food relative to a baseline in which the food was not devalued for the female. In

PSYCHOLOGICAL AND COGNITIVE SCIENCES

Fig. 1. Outline of the experimental procedures. Birds underwent each experiment—(A) specific satiety, (B) food sharing, and (C) observational specific satiety—in the order in which they are listed. Condition refers to whether the female was visible to the male during the prefeeding phase. In the (A) specific satiety and (C) observational specific satiety experiments as well as in (B, i) the seen condition of the food-sharing experiment, males could watch the females being prefed; while in (B, ii) the unseen condition of the food-sharing experiment, they had no visual access to the females during prefeeding. The prefeeding and test columns depict the type of food (MD = maintenance diet, W = wax moth larvae, M = mealworm larvae) and quantity (when applicable) given to each bird, with durations of the phases given in italics.

the food-sharing experiment, the desire-state of the females was manipulated by giving them either MD, W, or M, whereas males always had MD to keep their desire constant across trials (Fig. 1 B, i). Similarly to the specific satiety experiment, because of inter-individual variation in the amount of sharing bouts and in the preference to share one food over the other, it was crucial to compare the sharing pattern in the test trials (females prefed W and M) to that shown in the baseline (females prefed MD). Males watched the females being prefed in an adjacent compartment through a wire-mesh window covered by a transparent screen (seen condition). When the screen was removed, the males were given 20 opportunities to choose between a single W and M that they could then share with the females through the wire-mesh window (Movie S1).

Males responded to the current desire-state of the females; they shared a lower proportion of W relative to the baseline (female prefed MD) after the female had been prefed W than after she had been prefed M (Fig. 3A; exact Wilcoxon signed-rank test, $n = 7$, $T = 3$, $P_{one-tailed} = 0.05$; Tables 1 and 2). Crucially, because males never had visual access to the females during the test phase of the specific satiety experiment (Fig. 1A), the decrease in the males'

sharing of the prefed food could not be explained by any prior experience of the females' response to prefeeding in this context.

It is possible that the females indicated their food preference behaviorally during the test phase and that these cues influenced the males' sharing behavior. For example, at the moment when the male was making his choices of what food to share with his mate, the female could have been begging more intensely for one of the foods. Alternatively, immediately after a sharing bout, the female's behavior could have indicated either acceptance or rejection of the food that had just been given to her by the male. Many previous studies have failed to adequately control for this "stimulus-bound behavior reading" (26). To test this possibility, we included a condition in which the males could not see the females and what they ate during the prefeeding phase (unseen condition; Fig. 1 B, ii), such that the only cue available to them on which to base their decision of what to share was the females' behavior during the test phase. The procedure was identical to the seen condition in all other respects. To ensure that females experienced specific satiety in both the seen and unseen conditions, we compared the amount eaten during the prefeeding phase in these conditions and the specific satiety experiment (exact Friedman test, df = 5, prefed W:
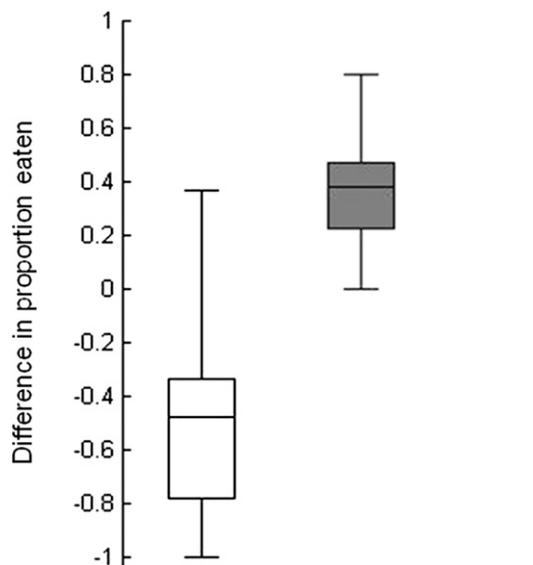
Ostojić et al.

Fig. 2. Average difference in the proportion of W eaten in the specific satiety experiment between the prefed W and the prefed MD trials (white box) and between the prefed M and the prefed MD trials (gray box). Boxes show the median and upper and lower quartiles (75% and 25%) of the data; whiskers show the maximum and minimum values. For individual data, see Tables 1 and 2.

$\chi^2 = 4, P > 0.05$, prefed M: $\chi^2 = 7.58, P > 0.05$). We can therefore be confident that the females' behaviors (as affected by how much they had eaten of a particular food) did not differ between the seen and the unseen conditions. However, a comparison between the seen and unseen conditions revealed a difference in the males' sharing behavior (Fig. 3A; exact Wilcoxon signed-rank test, $n = 7$, $T = 0, P_{one\text{-}tailed} = 0.01$). Therefore, the effect of decreasing sharing of the prefed food by the males in the seen condition cannot be explained by stimulus-bound behavior reading (26). In short, the males needed to observe what the female had eaten during the prefeeding phase; simply observing her behavior during the test phase did not provide them with sufficient information to ascertain which food she desired most.

There are at least two reasons it is perhaps not surprising that the female did not indicate her preference behaviorally to the male during the test phase. The first is that the act of sharing itself is likely to be of importance for the birds because in Eurasian jays,

food sharing is an important courtship behavior that plays a crucial role in the formation and maintenance of pair-bonds (27, 28). Consequently, the females might accept all foods offered by the male, regardless of their current desires. The second is that as a food-caching species, a female jay has the possibility to accept food shared by the male and then cache it for later consumption, reducing the likelihood that she would outright reject the food that was currently undesirable to her (29). Despite this, it remains highly likely that the male is motivated to share the food that is currently desired by his mate, for doing so would increase his value as a mate. Consider as a comparison a man giving his wife chocolates; the giving and receiving of chocolates is an important pair-bonding ritual, and as such the wife may be unlikely to reject the chocolates whether or not she currently wants them. However, a man that makes sure that he gives his wife the chocolates she currently really wants will improve his bond with her much more effectively.

Ascribing internal states to other individuals requires the basic understanding that others are distinct from the self and that others' internal states are independent from, and can differ from, one's own. Such self–other differentiation has been crucial in understanding children's state-attribution (2) and has also been identified as an important cognitive factor in empathy (22, 23). Without evidence for self–other differentiation, another possible explanation for the difference between the seen and unseen conditions in the food-sharing experiment is that males developed specific satiety themselves through watching the females being prefed on a particular food (hereafter observational specific satiety), and that their subsequent sharing behavior reflected their own, rather than the females', desire-state.

Demonstrating self–other differentiation behaviorally requires creating a situation within a given motivational system (in our case, food value) in which an individual's own desire-state is in direct competition with the desire-state of another social agent. In the case of the food-sharing experiment, the male's desire-state was kept constant as he was always prefed MD, whereas the female's was manipulated by prefeeding MD, W, or M. However, it is important to also provide evidence that an individual is capable of disregarding his or her own desire-state. Without this evidence, another possible explanation for the difference between the seen and the unseen conditions is that males developed specific satiety themselves through watching the females being prefed on a particular food and that their subsequent sharing behavior reflected their own, rather then the females', desire-state.

To test this possibility we ran an observational specific satiety experiment (Fig. 1C) in which the prefeeding phase was identical

Table 1. Individual data for the total number of W and M eaten by the males during the specific satiety and observational specific satiety experiments and the number of W and M shared in the seen and the unseen conditions of the food-sharing experiment

Experiment	Food prefed	Ayton		Caracas		Dublin		Lima		Lisbon		Pendleton		Wilson	
		W	M	W	M	W	M	W	M	W	M	W	M	W	M
Specific satiety	MD	3	12	27	9	10	0	100	21	26	0	21	10	13	15
	W	0	12	1	4	0	3	66	3	0	4	0	10	1	5
	M	4	0	9	0	6	0	100	0	4	0	35	2	11	2
Food sharing: Seen	MD	5	0	5	2	11	2	6	3	7	0	7	3	6	9
	W	6	2	1	2	6	1	1	0	3	2	3	2	3	5
	M	7	1	7	1	11	0	4	1	6	0	8	1	4	2
Food sharing: Unseen	MD	5	0	7	1	6	2	5	0	5	0	1	3	2	2
	W	5	1	3	0	7	1	7	0	3	0	3	2	5	5
	M	1	1	5	1	8	1	7	2	3	0	2	1	3	3
Observational specific satiety	MD	20	6	6	13	5	6	57	18	4	2	0	10	5	15
	W	10	8	3	15	10	0	100	3	2	3	2	13	8	14
	M	21	4	1	16	11	2	81	12	1	0	5	0	5	14

M, mealworm larvae; MD, maintenance diet; W, wax moth larvae. Table shows males. The food prefed column refers to the food type (MD, W, M) fed to each individual during the prefeeding phase of the experiment.

Ostojić et al.

Table 2. Individual data for the total number of W and M eaten by the females during the specific satiety experiment

Specific satiety	Food prefed	Adlington		Ohuruogu		Purchas		Quito		Rome		Wellington	
		W	M	W	M	W	M	W	M	W	M	W	M
	MD	28	8	4	7	5	10	19.5	13.5	10	7	11	12
	W	0	8	0	13	0	12	0	3	0	3	0	8
	M	4	0	6	0	7	0	6.5	0	3	0	23	0

M, mealworm larvae; MD, maintenance diet; W, wax moth larvae. Table shows females. The food prefed column refers to the food type (MD, W, M) fed to each individual during the prefeeding phase of the experiment.

to the prefeeding phase in the food-sharing experiment (Fig. 1 *B, i*). After prefeeding, the females were released back into the aviary and the males were given two bowls with W and M (equivalent to the test phase in the specific satiety experiment; Fig. 1 *A* and *C*). A difference in the males' eating behavior between the observational specific satiety and the specific satiety experiments (Fig. 3*B*; exact Wilcoxon test, $n = 7$, $T = 0$, $P_{one-tailed} = 0.01$; Table 1) negates the possibility that males developed observational specific satiety through watching the female being prefed on the test foods during the food-sharing experiment.

Discussion

Taken together, the results of the three experiments provide behavioral evidence that a nonhuman animal, the jay, flexibly caters

Fig. 3. Average difference in the proportion of W shared in the (*B, i*) seen and (*B, ii*) unseen conditions of the food-sharing experiment and eaten by the males in the (*A*) specific satiety and (*C*) observational specific satiety experiments between the prefed W and the prefed MD trials (white boxes) and between the prefed M and the prefed MD trials (gray boxes). Boxes show the median and upper and lower quartiles (75% and 25%) of the data; whiskers show the maximum and minimum values. For individual data, see Table 1.

for another individual's desire-state as induced by specific satiety. The behavioral criteria for self–other differentiation and against a stimulus-bound behavior reading account are satisfied by the data. Therefore, males must have used information obtained by watching the female being prefed to appropriately respond to the changes in her motivational state to then share with her the food that she was most likely to currently desire.

The results of the unseen condition negate the possibility that the males might have learned a simple rule (such as "do not feed what has just been eaten"). Learning about an action can only occur when that action is reinforced (regardless of the content of what is being learned). Therefore, in our case, for the male to learn when is an appropriate situation in which to feed the female different foods, he must have experience of the acceptance or rejection of certain foods by the female. As discussed earlier, the results of the unseen condition indicate that the female's immediate behavior when the male is sharing the food during the test phase is not sufficient to elicit the differential sharing pattern by the males: it is only in the seen condition that the male provides the food that the female desires. This difference between the seen and unseen conditions makes it highly unlikely that males would have been able to previously learn any rule for which the female's acceptance or rejection of his attempts at sharing would have acted as the reinforcement.

Additionally, it is highly unlikely that Eurasian jays possess an innate behavioral response to another's satiation. Specific satiety in animals relies on incentive learning, namely that individuals need to experience a particular food when they are sated on it to learn that its subjective value has been decreased through having been prefed on it (16, 17). Given that one's own specific satiety needs to be learned, it is not plausible that an innate rule would have evolved to provision for the specific satiety of another individual.

In summary, our data satisfy two crucial behavioral criteria for state-attribution: the males' sharing behavior was guided neither by their own desires nor by behavioral cues from the female at the time when males made the decision of what to share with her. The differential sharing of the test foods occurred only after males had had visual access to the females during the prefeeding stage (seen condition; Fig. 1 *B, i*). This finding has several implications. First, it emphasizes that within the belief-desire system, individuals explain and predict others' actions by reasoning about others' mental states. However, individuals must also have knowledge about behavioral and environmental contexts that causally affect the others' mental states (1). Second, in the absence of language, for nonhuman animals, these observable behavioral and external cues represent the only source of information by which they can attribute to others an internal life like their own (30). Unlike stimulus-bound behavior reading (26), such cues were only present during the prefeeding phase and were not directly observable by males at the time they had to make their decision of what food to share. It has yet to be established what information males acquire during watching the females being prefed and which mechanism enables them to use this information to inform their decision on what to share with the female in the subsequent test phase.

The behavioral and environmental information available to the males during the prefeeding phase consists of the female eating
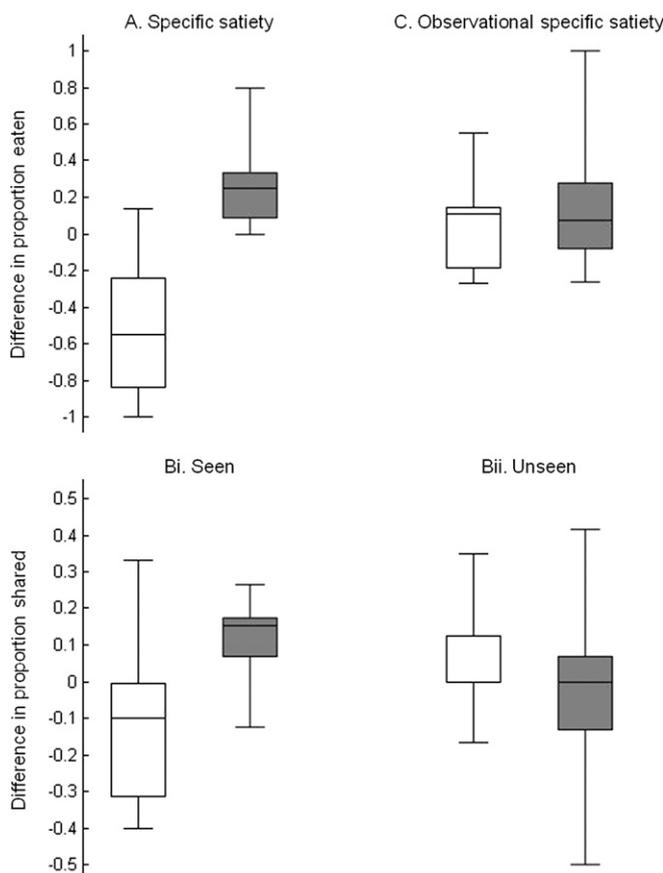
Ostojić et al.

one of the test foods. This represents the causal link that leads to a change in the female's desire toward that food. Potentially, the females' eating behavior might be perceived by the male as an otherwise unobservable specific satiety for that food. If future research could establish that specific satiety is not perceivable in the female's behavior during prefeeding, this would necessitate state-attribution on the part of the males to cater for the female's current desire. Conceivably, recent experience of their own specific satiety with the same foods in the same context (i.e., the specific satiety experiment) might have enabled the males to cater to their mate's changes in desire by means of experience projection. Experience projection is the ability to use one's own experiences and behavior to predict the experiences and behavior of another individual. This ability has been suggested to exist in a related corvid, the Western scrub-jay (*Aphelocoma californica*) (7).

The results of the current study present a crucial first step in demonstrating state-attribution. They fulfill the necessary behavioral criteria, namely ruling out behavior reading at the time of action and providing evidence of self–other differentiation. Our study suggests that the Eurasian jays' food-sharing behavior represents a useful paradigm within which to investigate whether these birds, and more generally nonhuman animals, might be capable of desire-attribution.

Materials and Methods

Subjects. Data from seven male-female Eurasian jay pairs were collected in the breeding seasons 2010–2012 (March–June). The experiments were approved by the University of Cambridge and conducted under the UK Home Office Project Licenses PPL 89/1975 and PPL 80/2519. Pairs included 14 Eurasian jays (7 males, 7 females) from two colonies (colony 1: $n = 8$, 4 y old; colony 2: $n = 6$, 3 y old). One male had different female partners between 2010 and 2011. The second female partner participated solely in conditions in which data were only collected for males. His partner from 2010 repaired with another, previously untested, male and this pair was tested in 2011. For the purpose of the analyses, data from the males in these two pairs are considered independent, whereas an average across 2010 and 2011 was calculated for all data concerning the female.

Colonies 1 and 2 were housed in two separate outdoor aviaries (20 × 6 × 3m) with indoor testing compartments (2 × 1 × 2 m) at one end that the birds could access from the aviary via opaque flap doors (0.5 × 0.5 m), which were opened and closed by the experimenter. Birds were fed a maintenance diet of soaked dog biscuits, cheese, seeds, nuts, and fruit and had ad libitum access to water.

Procedure. Testing took place in the compartments attached to the aviary. Each of our three experiments consisted of a prefeeding phase and a test phase (Fig. 1 A–C) and was preceded by ~2 h during which birds had no access to their maintenance diet. During testing, females and males were placed in separate, adjacent compartments that were joined by a wire mesh window. All pairs were tested only once in a day.

Specific Satiety Experiment. To ensure that jays had a specific satiety for our test foods, we investigated whether birds would respond to the prefeeding and therefore devaluation of a particular food by subsequently eating a smaller amount of that food relative to when this food was not devalued. We prefed birds on one food type—either MD, W, or M—and then gave them access to two bowls containing W and M (Fig. 1A). All birds started with being prefed MD (baseline), whereas the order of prefeeding the two test foods was counterbalanced across birds. The mesh window was covered by transparent Perspex to prevent food sharing from occurring during prefeeding and by opaque material during the test phase, such that birds could not observe the choices made by their partner.

We calculated the difference of the proportion of W eaten between the baseline (prefed MD) and the conditions in which birds were prefed one of the two test foods (prefed W and prefed M). If birds learned about their specific satiety to the two test foods during testing (17), we predicted that when the differences were compared, a decrease should be shown from the prefed M to the prefed W trials.

Food-Sharing Experiment. In this experiment, we investigated whether males would respond to the females' specific satiety by sharing fewer of the food items that had been devalued relative to the amount of that food shared

when it had not been devalued for the female. In the prefeeding phase of the food-sharing experiment, females ate either MD, W, or M, whereas males ate MD in all trials (Fig. 1B). During prefeeding, the mesh window was either covered by a transparent Perspex screen (seen condition; Fig. 1 B, i), or with opaque material (unseen condition; Fig. 1 B, ii). The order of the seen and unseen conditions was counterbalanced between pairs. All pairs started with the female being prefed MD (baseline), whereas the order of prefeeding the female the two test foods was counterbalanced across pairs. During prefeeding, in this and all experiments described, both M and W were present in the testing area to control for odor cues and were visible to the male in the seen condition of the food-sharing experiment. In the test phase of the food-sharing experiment, males were given 20 choices between W or M (Movie S1). The position of the foods was pseudorandomized with no food appearing on the same side on more than two consecutive trials. If the males did not make a choice within 30 s, the foods were removed. Each opportunity to make a choice was followed by a 40-s delay in which males could share with the female through the open mesh window (Fig. 1B).

We calculated the difference in the proportion of W shared by the males between the baseline (prefed MD) and the condition in which the females were prefed one of the two test foods (prefed W and prefed M). If males responded to the females' specific satiety to the two test foods, we predicted that when the above differences were compared, a decrease in the proportion of W shared should be shown from the prefed M to the prefed W trials.

In the seen condition, males could rely on both the information gained in the prefeeding phase and the information from the females' behavior during the test phase to inform their decision on what to feed her. In contrast, in the unseen condition, the only information available to the males was the females' behavior during the test phase. The procedure was identical to the seen condition in all other respects. Therefore, if an effect was found in the unseen condition and the males' sharing behavior did not differ between the seen and the unseen conditions, this would indicate that males are able to respond to the females' specific satiety by reacting to her behavioral cues [stimulus-bound behavior reading (26)]. If, however, the males' sharing behavior differed between the seen and the unseen conditions, this would indicate that using stimulus-bound behavior reading alone cannot account for the males' response to the females' specific satiety. Thus, seeing the female being prefed would be crucial for any effect found in the seen condition.

Observational Specific Satiety Experiment. Finally, we investigated the possibility that the males could have developed observational specific satiety by watching the females interact with one food type. Evidence that males did not develop specific satiety themselves through watching the females being prefed on a particular food is important for showing that the males' subsequent sharing behavior reflected their own, rather than the females' specific satiety (self–other differentiation). Two males in colony 1, which had been tested on specific satiety and food sharing in 2010, were tested on this experiment in 2011 (with an additional test of specific satiety to compare the data across years). All other pairs were tested on the observational specific satiety immediately after the food-sharing experiment. Here, birds were prefed in the same manner as the seen condition of the food-sharing experiment and the all pairs started with the female being prefed MD (baseline), whereas the order of prefeeding the female the two test foods was counterbalanced across pairs. Subsequently, the females were released into the aviary and the males were given access to two bowls containing W and M (homologous to the test phase of the specific satiety experiment; Fig. 1C).

We calculated the difference of the proportion of W eaten by the males between the baseline (females prefed MD) and the conditions in which females were prefed one of the two test foods (prefed W and prefed M). In accordance with the prediction that males did not develop observational specific satiety through watching the females being prefed the test foods, we expected the males' eating pattern in this experiment to differ to their eating pattern in the specific satiety experiment.

Analysis. All graphs show the difference in the proportion of W eaten or shared between the baseline (prefed MD) and trials in which one of the test foods had been prefed (prefed W and prefed M). Relating the results from the test trials to the performance during the baseline ensured that interindividual variation both in the amount of food eaten or shared as well as in general food preferences were taken into account. Because of the birds' general preference for the two test foods (both W and M) over MD, they are likely to eat more of the test foods than of the MD during prefeeding. Therefore, they might experience a higher general satiety in the test trials than in the baseline. This might lead to a decrease in the amount of food eaten or shared during the test phase. However, if they developed specific satiety (specific satiety and observational specific satiety experiments) or take the females' specific satiety into

account (food-sharing experiment), this decrease was predicted to be larger for the prefed and therefore devalued food than for the other food type.

The data were live scored by experimenter 1 (L.O.) for colony 1 and experimenter 2 (R.C.S.) for colony 2. A naive rater coded 51% of sharing bouts for which the recorded video allowed them to clearly see the sharing event. The same bouts were then coded by experimenter 1 who was blind to the condition in which the birds were tested at the time of rating. Interobserver reliability for the type of larvae shared by the male was high ($n = 94$, Cohen's $\kappa = 0.87$).

Because of the small sample sizes, data were analyzed using exact nonparametric tests (31). The main analyses were based upon clear predictions—specific satiety experiment: a decrease in the proportion of W eaten relative to the baseline (prefed MD) after birds had been prefed W (W devalued) compared with when birds had been prefed M (M devalued); and seen condition: a decrease in the proportion of W shared by the males relative to the baseline (females prefed MD) after females had been prefed W compared with when females had been prefed M. Our two controls for testing the behavioral criteria for state attribution required the comparison between test conditions. In accordance with the state-attribution hypothesis, the decrease in the proportion of W eaten from prefed M to prefed W (relative to the baseline) was predicted to be higher in the specific satiety than in the observational specific satiety experiment and predicted to be higher in the seen than in the unseen condition of the food-sharing experiment. Thus, all of the comparisons were calculated using directional exact Wilcoxon signed-rank tests (one-tailed P values). For all other analyses, for which there were no clear predictions tests were nondirectional (two-tailed P values). Alpha for all tests was set at 0.05.

1. Wellman HM, Bartsch K (1988) Young children's reasoning about beliefs. *Cognition* 30(3):239–277.
2. Bartsch K, Wellman HM (1989) Young children's attribution of action to beliefs and desires. *Child Dev* 60(4):946–964.
3. Perner J, Leekam SR, Wimmer H (1987) Three-year-olds' difficulty with false belief: The case for a conceptual deficit. *Br J Dev Psychol* 5:125–137.
4. Wellman HM, Cross D, Watson J (2001) Meta-analysis of theory-of-mind development: the truth about false belief. *Child Dev* 72(3):655–684.
5. Astington JW (2001) The future of theory-of-mind research: Understanding motivational states, the role of language, and real-world consequences. *Child Dev* 72(3):685–687.
6. Bugnyar T, Heinrich B (2005) Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proc Biol Sci* 272(1573):1641–1646.
7. Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414(6862):443–446.
8. Flombaum JI, Santos LR (2005) Rhesus monkeys attribute perceptions to others. *Curr Biol* 15(5):447–452.
9. Dally JM, Emery NJ, Clayton NS (2006) Food-caching western scrub-jays keep track of who was watching when. *Science* 312(5780):1662–1665.
10. Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? *Anim Behav* 61(1):139–151.
11. Kaminski J, Call J, Tomasello M (2008) Chimpanzees know what others know, but not what they believe. *Cognition* 109(2):224–234.
12. Schmelz M, Call J, Tomasello M (2011) Chimpanzees know that others make inferences. *Proc Natl Acad Sci USA* 108(7):3077–3079.
13. Shillito DJ, Shumaker RW, Gallup GG, Beck BB (2005) Understanding visual barriers: Evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Anim Behav* 69:679–687.
14. Buttelmann D, Call J, Tomasello M (2009) Do great apes use emotional expressions to infer desires? *Dev Sci* 12(5):688–698.
15. Hattori Y, Leimgruber K, Fujita K, De Waal FBM (2012) Food-related tolerance in capuchin monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-consumption. *Behaviour* 149:171–185.
16. Dickinson A, Balleine B (1995) Motivational control of instrumental action. *Curr Dir Psychol Sci* 4:162–167.
17. Balleine BW, Dickinson A (1998) The role of incentive learning in instrumental outcome revaluation by sensory-specific satiety. *Anim Learn Behav* 26:46–59.
18. Correia SPC, Dickinson A, Clayton NS (2007) Western scrub-jays anticipate future needs independently of their current motivational state. *Curr Biol* 17(10):856–861.
19. Tomasello M, Carpenter M, Call J, Behne T, Moll H (2005) Understanding and sharing intentions: The origins of cultural cognition. *Behav Brain Sci* 28(5):675–691, discussion 691–735.
20. Paal T, Bereczkei T (2007) Adult theory of mind, cooperation, Machiavellianism: The effect of mindreading on social relations. *Pers Individ Dif* 43:541–551.
21. Barrett HC, Cosmides L, Tooby J (2010) Coevolution of cooperation, causal cognition and mindreading. *Commun Integr Biol* 3(6):522–524.
22. Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci* 25(1):1–20, discussion 20–71.
23. de Waal FBM (2008) Putting the altruism back into altruism: The evolution of empathy. *Annu Rev Psychol* 59:279–300.
24. Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim Cogn* 4:269–280.
25. Penn DC, Povinelli DJ (2007) On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind.' *Philos Trans R Soc Lond B Biol Sci* 362(1480):731–744.
26. Penn DC, Povinelli DJ. The comparative delusion: The 'behavioristic'/'mentalistic' dichotomy in comparative Theory of Mind research. *Oxford Handbook of Philosophy & Cognitive Science*, eds Samuels R, Stich SP (Oxford Univ Press, Oxford), in press.
27. Lack D (1940) Courtship feeding in birds. *Auk* 57:169–178.
28. Goodwin D (1951) Some aspects of the behaviour of the jay *Garrulus glandarius*. *Ibis* 93:414–442.
29. Cheke LG, Clayton NS (2012) Eurasian jays (*Garrulus glandarius*) overcome their current desires to anticipate two distinct future needs and plan for them appropriately. *Biol Lett* 8(2):171–175.
30. Whiten A (1996) *When does behaviour-reading become mind-reading. Theories of theory of mind*, eds Carruthers P, Smith PK (Cambridge Univ Press, London).
31. Mundry R, Fischer J (1998) Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: Examples from animal behaviour. *Anim Behav* 56(1):256–259.

Ostojić et al.