This is the revised pre-print. During the revision process we changed the title. The original title was ‘Male Eurasian jays flexibly alter their food sharing in line with their partners’ choice’.

Investigating the flexibility of male Eurasian jays’ food-sharing behavior

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Abstract

Male Eurasian jays were previously reported to alter their food-sharing response in line with the specific satiety of their female partner. Here, we tested the flexibility of the same males' food-sharing behavior by testing whether they can process information from contextual cues that predict the opposite pattern of food shared to that observed in previous studies. In Experiment 1, we manipulated the amount of food eaten by the females in a choice context before males shared with them. In Experiment 2, we manipulated the identity of the non-chosen food that was available in a choice context before males shared with the females. In both experiments, males showed flexibility in their sharing pattern in a comparison between the experimental and control conditions. In Experiment 1, this observed pattern appears to be based on the males' response to the amount of food eaten by the female, and in Experiment 2, it appears to be based on the males' response to the choice context in which the female's eating took place. Although the experimental conditions in Experiments 1 and 2 were conceptual replications, the predicted pattern of food shared by the males was detected only in the latter. While replications are needed to test the generalizability and robustness of these results, the current study provides a first set of data in line with the hypothesis that the Eurasian jay males may be able to flexibly adjust their food-sharing behavior to contextual cues. Raw data are available at 10.5281/zenodo.3633986, and code and meta-data are available at <https://osf.io/n9rcd/>.

Keywords: cognition, flexibility, corvids, Eurasian jays, food sharing

Introduction

Food sharing is a behavior that is widely used to study social cognition in non-human animals, likely due to its existence in a wide range of species and its social nature (Vahed, 1998; Stevens & Gilby, 2004; Legg et al., 2015). In Eurasian jays, a species of corvid, food sharing has been used to study co-operative social strategies in Eurasian jays (Ostojić et al., 2013, 2014). Like many other species of birds in general (Galván & Sanz, 2011; Lack, 1940), and corvids in particular (Lack, 1940), male Eurasian jays are highly motivated to feed larvae to their female partners in beak-to-beak exchanges during breeding season (Goodwin, 1951, 1956; Lack, 1940). In previous food-sharing studies in Eurasian jays, males have been shown to alter the pattern of food shared depending on what their partner had been pre-fed (Ostojić et al., 2016a, 2014, 2013). These studies all focused on manipulating the female's desires for the test foods using the specific satiety phenomenon, where the continued consumption of a single food reduces the subsequent desirability of that food relative to others (Balleine & Dickinson, 1998; Havermans et al., 2009). To share in line with the female's satiety, the male must reduce how much of the sated food he gives to the female (relative to a novel food) compared to when she is sated on a different food type.

As such, the food-sharing pattern shown in experiments to date (Ostojić et al., 2013, 2014, 2016a) could theoretically result from a rigid rule where males are less likely to share food items that they have seen their partner eat recently (Ostojić et al., 2016b). Although no attempt has yet been made to measure Eurasian jays' food sharing in the wild, this behavior appears to be involved in courtship (Goodwin, 1951, 1956; Lack, 1940), and it is therefore likely to have a positive effect on reproductive success (Galván & Sanz, 2011; Stevens & Gilby, 2004). Food sharing may therefore be under strong evolutionary pressure, allowing rigid innate responses to females' desires to arise over successive generations.

In this study, we have considered this possibility by assessing the flexibility of the food-sharing response in male Eurasian jays. To do so, it was necessary to test whether males

flexibly adjust the pattern of food shared with their female partner to the context in which they see her eat the food, i.e. whether the males' cognitive systems process information from such contextual cues. Given that the previously observed sharing pattern was that of sharing *relatively less* of the food previously eaten by the female, the contextual cues had to be manipulated in such a way that the opposite sharing pattern would be predicted, i.e. sharing *relatively more* of the food previously eaten by the female (Ostojić et al., 2016b). Given that to develop specific satiety to a particular food, continuous consumption of that food is necessary (Balleine & Dickinson, 1998; Havermans et al., 2009), the first change in the contextual cues involved the number of food items eaten by the female. Consequently, in all experimental conditions in the current study the male saw the female eat a single item of a particular food, a quantity that should not induce specific satiety. In addition, eating one food item in the absence of any other food is not necessarily indicative of the likelihood that someone will choose that food over another in a future situation (Luo, 2011; Luo & Baillargeon, 2005, 2007). The same reasoning, i.e., that a choice context should be indicative of a volitional action, while a context in which only one item is accessible should not, has also been used in a study with capuchin monkeys (Prétôt et al., 2018). Thus, we also introduced a second change in contextual cues, i.e., we introduced a choice scenario. In all previous studies (Ostojić et al., 2013, 2014, 2016a), the male saw the female eat one food, although the other test food was also present in the testing area – but outside of the female's compartment – to control for simple visual and odour cues. In contrast, in the present study the female had access to two bowls and the male saw her eat from one of them only. Thus, the current study introduced a choice context, i.e., the male saw the female eat from one bowl while there was always also a second bowl available to her. This procedure was adopted to make it more likely that the female's behavior may be perceived as a choice between two available foods (Kamil, 2013), and has been used to study understanding of object- and goal-

directed actions in infants (Woodward 1998; 1999; Luo & Baillargeon, 2005, 2007; Biro & Leslie, 2007), non-human primates (Drayton & Santos, 2014; Wood et al., 2007), and dogs (Marshall-Pescini et al., 2014).

In Experiment 1, the two bowls always contained different foods: one bowl contained W (wax moth larvae, *Galleria mellonella*) and the other one contained M (meal worm beetle larvae; *Tenebrio molitor*). The experimental condition, in which each bowl contained one item of food (1v1 condition), was based on the contextual cues which have been identified as crucial for potential processing of preferences in infants (Luo, 2011; Luo & Baillargeon, 2005, 2007). In these violation-of-expectation studies, when a protagonist chose A while B was present, infants appeared to expect the protagonist to subsequently choose A over B. In contrast, when a protagonist chose A while B was not present or not visible, infants seemed to not expect that the protagonist will subsequently choose A over B (Luo, 2011; Luo & Baillargeon, 2005, 2007). In an equivalent manner, the experimental condition in Experiment 1 involved the male seeing the female eat one food item while one item of the other test food was also present: for example, the male saw the female eat one W while one M was also present. To directly test whether the males' food-sharing response in this situation is flexible, we designed a control condition, in which the female's eating behavior should have been more ambiguous: here, the male saw the female eat five items of one food type while five items of the other food type were also present (5v5 condition). Thus, although the choice context was kept the same as in the 1v1 condition, the amount of food eaten by the female was increased and thus mimicked more the situation from previous studies (Ostojić et al. 2016a, 2014, 2013), because the female may have started to develop specific satiety to the food that she was eating. Consequently, the crucial comparison concerned the food-sharing pattern between the condition in which the female ate one item (1v1 condition) and the

condition in which she ate five items (5v5 condition). If males process the information from the contextual cues, it was expected that the pattern of sharing relatively more of the food that the female has eaten would be stronger in the 1v1 condition than in the 5v5 condition. In addition, in line with this prediction, males were also expected to clearly show this effect, i.e. to share relatively more of the food that the female has eaten, in the 1v1 condition.

Experiment 2 was designed to directly test whether the choice context itself is being taken into account by the males. Experiment 1 was originally designed to test this and as such, the experimental condition involved a choice context. However, we subsequently realised that this does not mean that the design can actually provide evidence that the males are processing this cue: although unlikely, a potential positive result (i.e., males sharing relatively more of the food of which they had just previously seen the female eat one item and this effect being stronger in the 1v1 than in the 5v5 condition) could also result from males only attending to the type of food that the female was eating - and critically, how much of it - without having processed that a different type of food was also available. Thus, in Experiment 2, we directly tested whether the choice scenario itself is being taken into account by the males by keeping the female's choice constant but manipulating the context in which it occurred. In the experimental condition, which was a conceptual replication of the 1v1 condition in Experiment 1, the two bowls contained different foods: one bowl contained one W and the other one contained one M. Thus, the male saw the female eat one item of one type of food, while one item of the other type of food was also available ('different' condition). In the control condition, the choice scenario was kept the same but the identity of the second, available food was changed to be the same as the one that was eaten by the female: both bowls contained either one W or one M. Thus, the male saw the female eat one item of one type of food, while another item of the same food was available ('same' condition). Just like

eating one item of a particular food with no other food being available is not necessarily indicative of what the individual would subsequently choose (Luo, 2005; Luo & Baillargeon, 2005, 2007), eating one item of a food while another item of the *same* food is available, and there being no time to eat the second item, is not necessarily indicative of whether the individual would subsequently choose this food over another. Thus, similarly to the 5v5 condition in Experiment 1, the 'same' condition in Experiment 2 was ambiguous for the males and had no directional prediction regarding the males' sharing behavior. Consequently, the crucial comparison concerned the food-sharing pattern between the condition in which the female ate one item while one item of a different food was present ('different' condition) and the condition in which she ate one item while another item of the same food type was present ('same' condition). If males process the information from the contextual cues, it was expected that the pattern of sharing relatively more of the food that the female has eaten would be stronger in the 'different' than in the 'same' condition. In addition, in line with this prediction, males were also expected to clearly show this effect, i.e., to share relatively more of the food that the female has eaten, in the 'different' condition.

Experiment 1

In Experiment 1, the male saw the female eat different amounts of a particular food in a choice context. The choices of the female were controlled by coating one type of food in quinine, a substance that, in small concentrations, is distasteful to birds (Skelhorn & Rowe, 2006) to make it unlikely that the female would eat this unpalatable food. In the experimental condition, the female was presented with a choice between a single W and a single M (1v1 condition). In the control condition, she was presented with a choice between 5 W and 5 M (5v5 condition). Although in both conditions the female ate food in a choice context, the quantity of food eaten in the 5v5 condition may have led the female to start developing

specific satiety, such that in this condition, it should be ambiguous what food the female would subsequently prefer. In an ideal situation, to increase the power of the statistical test for the comparison between the conditions, both the experimental and the control condition should have directional and opposite predictions (Lakens & Caldwell, 2019), i.e. the control condition should not be merely ambiguous regarding its predictions about the males' behavior. This could be achieved by more directly mimicking the situation from previous studies, namely by giving the female much more than five food items to eat, such that it is ensured that she really does become sated on the food. However, such a procedure was not possible because it would have introduced confounds into the experimental design: the two conditions would not have differed only by the amount of food eaten, but also differed drastically in the length of the female's eating behavior and, crucially, by the fact that in the 1v1 condition, at the end of eating, no food would be in the bowl, while in the condition with the large quantity of food, food would still be left in the bowl. To ensure that, after the female had eaten, the food bowl was empty in both conditions, we considered what the largest quantity of food could be that all females were very likely to eat entirely. Data from pre-feeding phases of previous experiments (Ostojić et al., 2013, 2014, 2016a) showed that all females would eat at least five items of both food types, such that five was chosen as the number of food items in the control condition.

Methods

Subjects

Eight male-female pairs from two colonies (colony 1 = 4 pairs, colony 2 = 4 pairs) were tested in April and May 2014, during the breeding season in which food sharing takes place with highest frequency for the jays housed in our lab. These were all birds that were available to us for testing at the laboratory. These were all pairs of this species that were housed at the Sub-

Department of Animal Behaviour, University of Cambridge, at that time and that readily engaged in food sharing in the testing compartments at the time of testing. There was one more mated pair in colony 2, and this pair had participated in previous food-sharing studies (Ostojić et al. 2013, 2014). However, this pair did not reliably share food in the testing compartment in the year this study was conducted and thus was not tested (this was already a problem in the study reported in Ostojić et al., 2016). Colony 1 was tested by Edward Legg, and colony 2 by Ljerka Ostojić. All birds had previously taken part in food-sharing studies (Ostojić et al. 2013, 2014). The birds were housed in outdoor aviaries ($20 \times 6 \times 3\text{m}$) and tested in indoor compartments ($2 \times 1 \times 2\text{m}$). The birds were fed a maintenance diet of soaked cat biscuits, vegetables, seeds and fruit and had ad libitum access to water. The birds were tested once per day.

Procedure

To ensure that the birds were mildly hungry and thus motivated to eat food during the experiment, maintenance diet was removed approximately 2 hours before the start of testing. Birds were tested once per day between the hours of 9am and 4pm, and the timing of testing for each pair was kept as similar as possible between days to keep their motivation consistent. During testing, the male and female were in adjacent compartments with the mesh between them covered by transparent plastic sheeting. This procedure prevented the birds from sharing anywhere except at a window cut into the plastic at a specific location that was in clear view for the experimenter. Both the female's and the male's compartment contained a wooden platform at approx. 1m above the floor, which was positioned such that it was either side of the window between the two compartments. However, due to the fact that the mesh between the compartments was covered with transparent sheeting, the birds were able to see into each other's compartments from all positions.

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200 All birds received a baseline trial that consisted of a feeding phase and a sharing phase.
201 During the feeding phase, the male was able to see the female eat maintenance diet. The male
202 himself received no food. The feeding phase ended after the female ate once from the
203 maintenance diet (this was specified in frequency rather than in number of items eaten
204 because with the birds' maintenance diet, this is difficult to both observe and retrospectively
205 inspect). The female was given a maximum of 5 minutes, and if she did not eat within that
206 time, the trial was stopped (i.e., no test phase was conducted) and repeated on the next day.
207 Subsequently, the male could share with the female the two test foods (W and M) and this
208 test phase was conducted in the same manner as in the test trials. This baseline ensured that
209 the pairs were motivated to share with each other in the experimental set-up and in front of
210 the experimenter. The passing criteria required the male to take a minimum of 10 worms
211 from the experimenter (50%) and share with the female on at least two separate occasions
212 (two separate sharing bouts) during the sharing phase. Only pairs that passed this baseline
213 proceeded to the test trials.

214 Each of the two conditions (1v1 and 5v5) consisted of two trials, one in which the female ate
215 the W and one in which she ate the M. This gave a total of four test trials occurring across
216 four days. Each test trial consisted of a pre-experience phase with the female alone, followed
217 by a feeding phase and a test phase for which both the male and female were present (Figure
218 1). These phases were run consecutively on the same day. The order in which the male saw
219 the female eat one food item (1v1 condition) and five food items (5v5 condition) during the
220 feeding phase was counterbalanced across birds. The order in which the male saw the female
221 eat W and M during the feeding phase was randomised within a condition but kept the same
222 across both conditions for each pair.

At the start of each trial, in the pre-experience phase, the female was presented with W and M in the male's absence (female in the testing compartment, male in the aviary). One type of food had previously been coated in a 2% quinine solution to make it unpalatable (Skelhorn & Rowe, 2006). W were coated directly in quinine, whereas M were first dipped in a 70% ethanol solution to prevent the quinine from being washed off the waxy cuticle (Jones et al., 2013). The food that was not coated in quinine was coated in water to mirror the 'wet' appearance of the quinine-coated food. Once the female had taken at least one item from each bowl the trial moved on to the feeding phase. If the female did not take the worms within 5 minutes the trial was stopped (no feeding and test phases conducted) and repeated on a subsequent day. No female required repeated trials. This pre-experience with quinine was given to increase the likelihood that the female would choose to eat the target (i.e., non-quinine treated) food during the subsequent feeding phase.

In the following feeding phase, the male was brought into the adjacent compartment. A transparent plastic barrier over the window prevented the birds from sharing food with each other at this stage. The female was presented with two bowls containing either one of each type of food (1v1 condition) or five of each type of food (5v5 condition). Again, in one bowl, the food was coated in quinine, and in the other one in water. The bowls were shown clearly to the male before being positioned in the female's compartment. To control for odor cues, a bowl with both types of food covered in quinine was present in the testing room but was placed outside the female's compartment and was not visible to the male. The male could watch the female while she ate, and the bowls were shown to the male when the bowls were removed from the female's compartment. Although male jays tend to closely attend to their female partners during breeding season, the male himself was given no food to ensure that he would not be distracted when the female ate her food. If the female took a food item that was not in line with her experience of the quinine, or if the female did not eat all the food in the

248 bowl within 5 minutes, the trial was stopped (no test phase conducted) and repeated on a
249 subsequent day. Across all trials and birds, there were three trials that had to be repeated.
250 After the female's eating, the transparent plastic barrier between the compartments was
251 removed and perches were placed onto the mesh window in both compartments to facilitate
252 sharing.

253 In the test phase, the male was presented with 20 choices of a single W versus a single M. For
254 six of the males the choices were held by hand against the mesh of the compartment (Hoy,
255 Romero, Caracas, Lima, Wilson and Pendleton), for males who did not take food by hand
256 (Lisbon and Dublin) the food items were placed on the wooden platform inside of the
257 compartment. The order of presentation was pseudo-randomized such that the same type of
258 food was not presented on the same side for more than two consecutive trials. Once the male
259 took one food, the other food was removed. If no choice was made within 30 seconds both
260 foods were removed. Each choice presentation was followed by a 40 second inter-choice
261 interval, in which the male could either eat, cache, or share the food with the female through
262 the mesh window. This interval was maintained even when the male made no choice of food.
263

Condition		Pre-Experience		Feeding			Test	
1v1	Female only (male not present)		Female		Male		Choice	Share
	water	quinine	target	other				
	W	M	1W	1M	/			
	M	W	1M	1W	/		1W vs. 1M
5v5	W	M	5W	5M	/			
	M	W	5M	5W	/			
		$\longrightarrow$		$\longrightarrow$			$\longrightarrow$	$\longrightarrow$
		until at least one of each food items taken (5 min max)		until target food item(s) eaten (5 min max)			30 sec (max)	40 sec
							20 trials	

Figure 1. Outline of the experimental procedure in Experiment 1. ‘Condition’ refers to the number of food items that the female ate during the feeding phase. The order in which the birds experienced the two conditions (1v1 and 5v5) was counterbalanced across birds. ‘Pre-experience’ refers to the phase in which the female only was in the testing compartment. ‘Water’ refers to which food items were – during this pre-experience phase – coated in water and was thus palatable, while ‘quinine’ refers to which food items were coated in quinine and thus tasted aversive to the female. ‘Feeding’ refers to the phase in which the male saw the female eat a specific food. The ‘female’ column shows which food the female ate (‘target’) and which other food was present and thus available to her but was not eaten (‘other’). In this experiment, the food item(s) given under the ‘target’ column were coated in water and food item(s) given under the ‘other’ column were coated in quinine – corresponding to which food items the female had experienced as being coated in water and quinine in the pre-experience phase. The ‘/’ under the ‘male’ column denotes that the male was not given any food during the feeding phase such that he was not distracted from watching the female eat. The ‘test’ column denotes which food the male could choose from (‘choice’) and that he was subsequently given the opportunity to share with the female. W = wax moth larvae, M = mealworm beetle larvae. Where applicable, duration and number of trials are given in italics.

Reporting

Given that the study was not pre-registered, in the following sentence we provide a transparency statement (‘21 word solution’) as proposed by Simmons et al. (2012). We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Analysis

The male's sharing was live-coded by the experimenter, recording the number of sharing events and whether the shared item was a W or M. The experimenter was not blind to the pre-feeding condition, because this procedure requires multiple experimenters that the birds are familiar with to be available to do the testing. In a previous study, we found that the males' choices of food and the males' sharing pattern are not likely to be explained by experimenters' expectancies, because experimenters blind to the condition (i.e., what food the female was pre-fed) replicated the main results of a previous food-sharing study ('seen' condition in Ostojić et al., 2013) The sharing phase for each condition was also recorded on video.

The males' food-sharing responses were measured using the proportion of W shared out of total number of items shared: $W/(W+M)$. The proportion of M shared is the inverse of this value and therefore does not alter the output of the analysis. This proportion was compared between the two test trials within each condition using two-tailed Wilcoxon signed rank tests. The difference between these two trials was then calculated $[W/(W+M)]_{M \text{ eaten}} - [W/(W+M)]_{W \text{ eaten}}$ and this difference score was compared between the two conditions (1v1 and 5v5) using a further two-tailed Wilcoxon signed rank test. Two-tailed tests were chosen rather than one-tailed tests as there was no a-priori reason to expect that the males' sharing pattern would follow one specific direction. Raw data are available at 10.5281/zenodo.3633986, and code and meta-data are available at <https://osf.io/n9rcd/>.

If the males' food-sharing behavior is flexibly adjusted to contextual cues provided by the environment in which the female is seen eating a particular food – in this case, the difference in the food eaten by the female in a choice scenario - the difference score was expected to be higher after the female ate one food item (1v1 condition) than after the female ate five food

items (5v5 condition). In addition, in the 1v1 condition, males were also expected to share a higher proportion of W after the female had eaten one W than after she had eaten one M.

Results and discussion

A comparison between the experimental and control conditions detected a statistically significant difference in the predicted direction, i.e., a higher difference score after the female had eaten one food item (1v1 condition) than after she had eaten five food items (5v5 condition; two-tailed Wilcoxon, $V = 26$, $p = 0.047$, 95% CI [0.03, 0.47], $r = 0.703$; see Figure 2). A comparison of the proportion of W shared between the two test trials (W eaten and M eaten) in the experimental condition (1v1 condition) did not detect a statistically significant difference in the predicted direction (two-tailed Wilcoxon signed rank test, $n = 8$, $V = 20$, $p = 0.063$, 95% CI [-0.14, 0.55], $r = 0.659$). It is in this condition that the female's eating behavior should have served as a cue as to which food type she would likely subsequently choose over the other. An exploratory analysis of the control condition (5v5 condition) did not detect a statistically significant difference in the proportion of W shared between the two test trials (two-tailed Wilcoxon, $n = 8$, $V = 8$, $p = 0.999$, 95% CI [-0.30, 0.25], $r < 0.001$). Thus, to the extent that the detected difference in the pattern of food shared between the two conditions can be said to be due to the experimental manipulation, the results may be taken to mean that these males flexibly adjusted their sharing behavior to the quantity of food eaten by the female. However, the results reported for the experimental condition suggest that the same conclusion is not permitted regarding the males' response to the choice context in which the female's eating took place.

Figure 2: Raincloud plot showing the proportion of W shared out of total food items shared in each test trial ('female ate M' and 'female ate W') in the 1v1 (left panel) and the 5v5 (right panel) conditions. Central tendency and error of the data are shown in a box plot: boxes show the median and upper and lower quartiles (75% and 25%) of the data, whiskers show the distance of 1.5 times from the inter-quartile range (IQR). Jittered raw data are shown for each individual male, with lines connecting data from the same male in the two test trials. Grouped illustration of the data shows the un-mirrored probability density functions (PDF) for each condition, plotted against the redundant data axes.

Experiment 2

Experiment 2 was designed to directly test whether the choice context itself is being taken into account by the males. As explained in the introduction, although Experiment 1 was originally designed to test this, we subsequently realized that this experiment is not actually able to provide empirical evidence for it, because the males might only be attending to what food and how much of it the female was eating, without having processed that a different type of food was also available. Indeed, the observed difference in the sharing pattern between when the female ate one item of a food (1v1 condition) and when she ate five items of a food (5v5 condition) can also be explained by the males only taking into account how

much of a particular food the female had eaten. In addition to the above consideration, males did not share a higher proportion of W after the female had eaten one W than after she had eaten one M (1v1 condition), which was the pattern that was expected had the males processed the information about the choice context.

In Experiment 2, we thus conducted a conceptual replication –with the same birds - of the 1v1 condition from Experiment 1 and contrasted this experimental condition with a control condition in which the female also ate one food item while another food item was available but where both items were of the same food type. This control condition was designed based on violation-of-expectation studies that showed that infants' response to others' preferences appears to go beyond simple statistical associations between actions and outcomes (Luo, 2011; Luo & Baillargeon, 2005, 2007). For example, if A is chosen when B is present infants appear to expect the protagonist to subsequently choose A over B, whereas if A is chosen when B is not present or not visible, they do not expect that A will be chosen over B. Such responses cannot be explained by simple associative processes, as - in both cases - the protagonist is equally associated with A. The infants appeared to be sensitive to the presence or absence of object B when the choices are being made, responding with 'surprise' only when the protagonist's previous choices were informative about which object was preferred over the other (Luo, 2011; Luo & Baillargeon, 2005, 2007).

The procedure of Experiment 2 was based on a previously pre-registered experiment designed by Brecht et al. (2016). Note however that, due to this having been the lab's first pre-registration, this pre-registration covered the methods and hypothesis tested but did not include an analysis plan. In the 'different' condition, the female was presented with two items of different foods (W vs M) during the feeding phase, whereas in the 'same' condition, the

female was presented with two items of the same food (W vs W; M vs M). Eating W in the 'different' condition and eating W in the 'same' condition should lead to equivalent association between the female and W. Thus, any differences in sharing pattern between the test trials in the 'different' condition and those in the 'same' condition could not be explained by the interaction between the female and the chosen food. In order for there to be a difference between the conditions the male must additionally take into account the identity of the second food (W or M), i.e., the choice context.

Methods

Subjects

Six male-female pairs from the two colonies (colony 1 = 2 pairs, colony 2 = 4 pairs) were tested in April and May 2018. These were all birds that were available to us for testing at the laboratory. Birds from both colonies were tested by Rachel Crosby. All pairs had participated in previous food-sharing experiments. There were two fewer pairs than in Experiment 1 because three birds from these pairs died of natural causes in the intervening period (Wilson – June 2014; Ohuruogu – July 2014, Pendleton - January 2017). The birds were housed and fed as described in Experiment 1. The birds were tested once per day.

Procedure

The birds were tested using the same procedure as described in Experiment 1, except for the differences outlined below. Colony 1 was tested between the hours of 10am and 1pm and colony 2 between 9am and 12pm. Each of the test trials consisted of a feeding phase followed by a test phase, run consecutively on the same day (Figure 3). In the feeding phase, the female was presented with two food items placed directly on the wooden platform in the

testing compartment. The two foods were one W and one M ('different' condition) or two foods of the same food type, either two W or two M ('same' condition).

The method used to manipulate the females' eating differed from the procedure that was pre-registered on the Open Science Framework (Brecht et al., 2016). The pre-registration suggested coating one type of worm in quinine, but instead we chose to exploit the birds' natural side bias for picking the worm to their right rather than to their left. This side bias was exhibited by the birds during training sessions with the experimenter who conducted this experiment. The 'different' condition was therefore a conceptual replication, albeit with the same birds, of the 1v1 condition in Experiment 1, the only difference being the manipulation of the females' eating through side biases instead of quinine. This change was made due to pilot trials in which the females would not take further worms following exposure to quinine-coated worms. This behavior may have been a consequence of their experiences with quinine in previous experiments. If a female did not eat the targeted food item, the trial was aborted (no test phase conducted) and repeated on the subsequent day. No trials were repeated due to this criterion; while on one trial, the female ate the food item on the left, the test phase was conducted and the planned order of trials (female ate W and female ate M) according to the counterbalancing for this pair was reversed (i.e., this happened for the first of the two test trials within a condition such that such a reversal was possible).

The subsequent test phase was conducted in the same manner as described in Experiment 1, except that here, in Experiment 2, there were two criteria that the birds had to pass for their data to be included in the analysis. Males were required to take a minimum of 10 worms from the experimenter (50%) and were required to share at least three worms with the female across the duration of the sharing phase. If these criteria were not met in a trial, the trial was repeated on a subsequent day. These criteria were introduced because the experimenter conducting Experiment 2 was a different one to the one in Experiment 1 and one with whom

the birds were not as familiar. Across all trials and birds, eight trials had to be repeated, three of them because the first criterion was not met, and five because the second criterion was not met.

Condition		Feeding		Test	
		Female	Male	Choice	Share
		target	other		
different		1W	1M	1W vs. 1M
		1M	1W		
same		1W	1W		
		1M	1M		
		<div> <div></div> <div></div> </div> <i>until target food item eaten (5 min max)</i>		<div> <div></div> <div></div> </div> <i>30 sec (max)</i>	<div> <div></div> <div></div> </div> <i>40 sec</i>
				<i>20 trials</i>	

Figure 3. Outline of the experimental procedure in Experiment 2. 'Condition' refers to whether the female was given items of two different foods ('different') or whether she was given items of the same food ('same') during the feeding phase. The order in which the birds experienced the two conditions ('different' and 'same') was counterbalanced across birds.. 'Feeding' refers to the phase in which the male saw the female eat a specific food. The 'female' column shows which food the female ate ('target') and which other food was present and thus available to her but was not eaten ('other'). In this experiment, the food item given under the 'target' column was positioned to the right of the female, while the food item under 'other' was positioned to her left. The '/' under the 'male' column denotes that the male was not given any food during the feeding phase such that he was not distracted from watching the female eat. The 'test' column denotes which food the male could choose from ('choice') and that he was subsequently given the opportunity to share with the female. W = wax moth larvae, M = mealworm beetle larvae. Where applicable, duration and number of trials are given in italics.

Reporting

Given that no detailed procedure and no analysis plan were pre-registered, in the following sentence we provide a transparency statement ('21 word solution') as proposed by Simmons et al. (2012). We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Analysis

Data were live scored by Rachel Crosby, who was – just like the experimenters in Experiment 1 – not blind to the experimental manipulations. To calculate inter-observer reliability, the sharing events were also coded from the recorded video by two coders (Rachel Crosby and Ben Farrar). The fixed angle of the camera made it very difficult to judge which worm type was shared in the majority of the sharing events. Out of a total of 166 shared worms both experimenters were able to record the worm type shared for only 66 of them (39.8%). From the events that both experimenters coded they were in agreement on 55 of them (87.3%). Overall this means that only 33.1% of all sharing events were agreed by both video coders. Furthermore, of the 55 events for which the video coders were in agreement, 7 of these agreements contrasted with the live coding. Similar problems with video coding have been identified in previous food-sharing studies with video recordings providing a clear view of just 51% of sharing events in the original study (Ostojić et al., 2013). In this study, the authors stated that inter-observer reliability between the two video coders was high for those events that could be clearly seen, but did not actually compare the video coding to the live coding. Considering that the live coding was the source of the data used in the analysis and the results, this finding therefore does not provide any measure of the reliability of the analysed data. However, a later study in which the live coder was blind to condition found similar results to the original study ('seen' condition in Ostojić et al., 2013), suggesting that the live coder's accuracy is not biased by their knowledge of the experiment's predictions

(Ostojić et al., 2016a). Given the issues with the video coding, the live coding appears to be the best possible option to use in the analysis. It is likely that the difficulty in reaching an agreement between the video and live coding is due to the low quality of the videos used for video coding and the nature of beak to beak sharing where the item shared can easily be obscured from the view of the camera. Importantly, in subsequent years, the birds have been trained to share food in front of GoPro cameras that were installed inside the testing compartments, such that in future studies, the above problems should not be a limiting factor anymore.

The males' food-sharing responses were measured and indexed in the same way as described in Experiment 1. Raw data are available at 10.5281/zenodo.3633986, and code and meta-data are available at <https://osf.io/n9rcd/>.

If the males' food-sharing behavior is flexibly adjusted to contextual cues provided by the environment in which the female is seen eating a particular food, namely the difference in the food types available to the female in a choice scenario, the difference score was expected to be higher after the female had a choice between two items of different foods ('different' condition) than after the female had a choice between two items of the same food ('same' condition). In addition, in the 'different' condition, males were also expected to share a higher proportion of W after the female had eaten one W than after she had eaten one M.

Results and discussion

A comparison between the experimental and the control conditions detected a statistically significant difference in the predicted direction, i.e., a higher difference score after the female had a choice between two items of different food types ('different' condition) than when she had a choice between two items of the same food ('same' condition; two-tailed Wilcoxon, $n = 6$, $V = 21$, $p = 0.031$, 95% CI [0.07, 0.83], $r = 0.879$, Figure 4). A comparison between the

two test trials (W eaten and M eaten) in the experimental condition ('different' condition) detected a statistically significant difference in the predicted direction, i.e., a higher proportion of W after the female had eaten the W than after the female had eaten the M (two-tailed Wilcoxon signed rank test, $n = 6$, $V = 21$, $p = 0.031$, 95% CI [0.08, 0.83] $r = 0.879$). An exploratory analysis of the control condition ('same' condition) did not detect a statistically significant difference in the proportion of W shared between the two test trials (two-tailed Wilcoxon, $n = 6$, $V = 10$, $p = 0.625$, 95% CI [-0.30, 0.16], $r = 0.20$). Thus, to the extent that the detected difference in the pattern of food shared between the two conditions as well as the difference detected in the experimental condition can be said to be due to the experimental manipulations, the results may be taken to mean that in this experiment, the males flexibly adjusted their sharing behavior to the choice context in which the female's eating took place.

Figure 4: Raincloud plot showing the proportion of W shared out of total food items shared in each test trial ('female ate M' and 'female ate W') in the 'different' (left panel) and the 'same' (right panel) conditions. Central tendency and error of the data are shown in a box plot: boxes show the median and upper and lower quartiles (75% and 25%) of the data, whiskers show the distance of 1.5 times from the inter-quartile range (IQR). Jittered raw data are shown for each individual male, with lines connecting data from the same male in the two test trials. Grouped illustration of the data shows the un-mirrored probability density functions (PDF) for each condition, plotted against the redundant data axes.

The difference in the observed sharing patterns between the experimental and control conditions indicates that the males' sharing cannot be explained only by a simple association between the female and the eaten food type. The female's action towards the chosen food was identical in both conditions ('different' and 'same'), with the identity of the second food being the only difference. If the males' sharing were based only on an association between the female and the chosen food item, the same pattern would be expected regardless of what other food was available at the time when the female ate a particular food. Furthermore, this pattern of results also likely cannot be explained by the female's behavior indicating her preference during the sharing phase as the females' choices were artificially manipulated. The female's choices resulted from her side bias rather than her true preferences, meaning that any preference-indicating behavior during sharing would not necessarily be aligned with her choices. These results therefore show that the males take into account the identity of the other food present at the time of choosing.

The 'different' condition of Experiment 2 is essentially a conceptual replication of the 1v1 condition in Experiment 1. However, while a statistically significant flexible sharing pattern in the predicted direction in this situation was detected in Experiment 2, this was not the case in Experiment 1. One possible explanation for this could be the different method used to manipulate the females' choices: the aversive substance quinine or the females' natural side biases, although there are no a priori reasons to assume that these different manipulations

should lead to different behavioural responses by the males. Critically, in neither manipulation should the female's behavior be suggestive of her real preference for the food items. Thus, any differences in results may be more indicative of their reliability or repeatability. Here, the difference in the results is likely to be a consequence of the small sample size, and inter-individual variation. The only male in the 1v1 condition that did not show the predicted response to the female's choices was Pendleton, and this bird was not included in Experiment 2 as he died of natural causes in January 2017. As a result of the small sample size, the exclusion of this single bird may explain the difference between Experiment 1 (1v1 condition) and the conceptual replication in Experiment 2 ('different' condition). Finally, given the lack of a direct comparison of the pattern observed in the experimental condition between the two experiments, paired with low power of the statistical tests, as well as low sensitivity (i.e., wide confidence intervals) in both experiments, it is problematic to interpret the results as being clearly different (Simonsohn, 2015).

General Discussion

In this study, we investigated the flexibility of male Eurasian jays' food-sharing behavior by testing whether males process different information from contextual cues when sharing food with their female partner. In Experiment 1, the results were mixed. Observed differences in the pattern of food shared indicate that the food shared by the tested males may have been a response to the quantity of food eaten by the female prior to sharing with her. However, given the lack of a statistically significant difference in the males' sharing behavior in the experimental condition, the data from this experiment were not in line with the males' sharing behavior having been a response to the choice context in which the females eating took place. In Experiment 2, observed differences in the experimental condition and between the experimental and control conditions indicate that the food shared by the tested males may

have been a response to the choice context. In addition, unlike in Experiment 1, the predicted pattern in the experimental condition itself was detected in Experiment 2.

The patterns observed across these two experiments contrast with the response seen in previous food-sharing studies with the same males (Ostojić et al., 2013, 2014, 2016a). All previous experiments involved manipulation of the female's desires via specific satiety, and there, males responded by sharing relatively *less* of the food they had seen the female eating. The pattern shown in this study appears to be the exact opposite, with males sharing relatively *more* of the food they had seen the female eating. The tested males were the same birds. Thus, the current study suggests that these males do not always respond by rigidly sharing less of the food their partner has eaten, but rather that they respond differently in different scenarios. Given that some of the previous food-sharing studies with these jays tested what cues the males respond to when feeding the female to attempt to differentiate between different cognitive mechanism that may underlie the males' behavior (Ostojić et al., 2013), it is important to note that this was not the aim of this study. Consequently, the current results are not able to clarify which mechanism might underlie the behavioral flexibility reported here.

All food-sharing studies in Eurasian jays in our lab have so far been conducted with the same birds. In addition, all these studies, including the current one, were conducted with a relatively small sample size. Consequently, it is necessary to be aware of generalization constraints that the results reported here face: until other Eurasian jay pairs can be tested using the same procedures, there will be no data available that would allow inferences regarding the generalizability of the results. At least some behavioral patterns may not be specific to this group of Eurasian jays, given that a study with wild New Zealand robins

reported the same food-sharing pattern (Shaw et al., 2017) as the one observed in the Ostojić et al. (2013) study. A second problem is that the small sample size, coupled with the design of the experiments in which there is only one trial per manipulation and – in this study – ambiguous control conditions, lead to low power of the statistical tests. Low power affects both false negative and false positive rates, however this does not say anything about the likelihood of any single finding being false (Button et al., 2013). Given that sample sizes in research like this are likely to always or often be constrained, one way in which power could be increased would be to conduct multiple trials to increase the precision of estimates. To avoid carry-over effects, loss of motivation to participate in the trials, or loss of attention to the food eaten by the female, one way to conduct multiple trials, and at the same time increase the generalizability of the results, would be to conduct the food-sharing experiments with multiple food pairs. Such a procedure with multiple trials with new object pairs has been implemented in a similar experiment by Drayton and Santos (2014). Although this is something we considered, we were faced with the problem that the Eurasian jays in our lab did not reliably share foods other than W and M in the testing compartments when we tested this.

In summary, the current findings are important because they provide the first data in Eurasian jays that address the question of the flexibility of the males' food-sharing behavior. However, these data cannot yet be used for any strong inferences regarding the above question. The observed patterns indicate that tested Eurasian jay males may have responded to the quantity of the food eaten by the female and the choice context in which her eating took place just before the sharing event. The replicability, and generalizability of these results will have to be further tested (ideally with different birds, and in different laboratories) for stronger

616 inferences regarding this flexibility of male Eurasian jays' food-sharing behavior to be
617 possible.

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Author Contributions

Rachel M Crosby contributed to acquisition of funding, conceived and designed Experiment 2, performed the experiments for Experiment 2, analyzed the data, prepared figures and code, authored the original draft of the paper, authored and reviewed drafts of the paper, approved the final draft.

Edward W Legg contributed to acquisition of funding, conceived and designed Experiment 1, performed experiments for Experiment 1, prepared code, reproduced results, authored or reviewed drafts of the paper, approved the final draft.

Katharina F Brecht contributed to acquisition of funding, conceived and designed Experiment 2, prepared figures and code, authored or reviewed drafts of the paper, approved the final draft.

Michael T Mendl contributed to acquisition of funding, reviewed drafts of the paper, approved the final draft.

Ljerka Ostojić contributed to acquisition of funding, contributed to the design of the experiments, performed the experiments for Experiment 1, supervised research activity, authored the revised version of the manuscript, prepared figures, authored or reviewed drafts of the paper, approved the final draft.

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References

- Apperly, I. A., & Butterfill, S. A. (2009). Do humans have two systems to track beliefs and belief-like states? *Psychological Review*, 116(4), 953–970. <https://doi.org/10.1037/a0016923>
- Balleine, B. W., & Dickinson, A. (1998). The role of incentive learning in instrumental outcome revaluation by sensory-specific satiety. *Animal Learning & Behavior*, 26(1), 46–59. <https://doi.org/10.3758/BF03199161>
- Biro, S., & Leslie, A. M. (2007). Infants' perception of goal-directed actions: development through cue-based bootstrapping. *Developmental Science*, 10(3), 379–398. <https://doi.org/10.1111/j.1467-7687.2006.00544.x>
- Brecht, K. F., Ostojić, L., Legg, E. W., & Clayton, N. S. (2016). Working title: Can Eurasian Jays take into account the intention of their partner in a food-sharing context? Retrieved from <https://osf.io/sg3d6/>
- Button, K. S., Ioannidis, J. P. A., Makrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafo, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, 14, 365–376.
- Drayton, L. A., & Santos, L. R (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition*, 17, 689–700. <https://doi.org/10.1007/s10071-013-0700-5>
- Galván, I., & Sanz, J. J. (2011). Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds. *Behavioural Ecology*, 22, 1088–1095.
- Goodwin, D. (1951). Some aspects of the behaviour of the jay *Garrulus Glandarius*. *Ibis*, 93(4), 602–625. <https://doi.org/10.1111/j.1474-919X.1951.tb05462.x>
- Goodwin, D. (1956). Further observations on the behaviour of the jay (*Garrulus glandarius*). *Ibis*, 98(2), 186–219. <https://doi.org/10.1111/j.1474-919X.1956.tb03040.x>

- 684 Havermans, R. C., Janssen, T., Giesen, J. C. A. H., Roefs, A., & Jansen, A. (2009). Food
685 liking, food wanting, and sensory-specific satiety. *Appetite*, 52(1), 222–225.
686 <https://doi.org/10.1016/j.appet.2008.09.020>
- 687 Jones, R. S., Davis, S. C., & Speed, M. P. (2013). Defence Cheats Can Degrade Protection of
688 Chemically Defended Prey. *Ethology*, 119(1), 52–57. <https://doi.org/10.1111/eth.12036>
- 689 Kamil, A. C. (2013). Eurasian jays predict the food preferences of their mates. *Proceedings*
690 *of the Royal Academy of Sciences USA*, 110, 3719–3720.
691 <http://dx.doi.org/10.1073/pnas.1300515110>
- 692 Lack, D. (1940). Courtship feeding in birds. *The Auk*, 57, 169–178.
- 693 Lakens, D., & Caldwell, A. R. (2019, May 28). Simulation-based power-analysis for factorial
694 ANOVA designs. <https://doi.org/10.31234/osf.io/baxsf>
- 695 Legg, E. W., Ostojić, L., & Clayton, N. S. (2015). Food sharing and social cognition. *WIREs*
696 *Cognitive Science*, 6(3), 119–129.
- 697 Luo, Y. (2011). Three-month-old infants attribute goals to a non-human agent.
698 *Developmental Science*, 14(2), 453–460. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-7687.2010.00995.x)
699 [7687.2010.00995.x](https://doi.org/10.1111/j.1467-7687.2010.00995.x)
- 700 Luo, Y., & Baillargeon, R. (2005). Can a self-propelled box have a goal? Psychological
701 reasoning in 5-month-old infants. *Psychological Science*, 16(8), 601–608.
702 <https://doi.org/10.1111/j.1467-9280.2005.01582.x>
- 703 Luo, Y., & Baillargeon, R. (2007). Do 12.5-month-old infants consider what objects others
704 can see when interpreting their actions? *Cognition*, 105(3), 489–512.
705 <https://doi.org/10.1016/j.cognition.2006.10.007>
- 706 Marshall-Pescini, S., Ceretta, M., & Prato-Previde, E. (2014). Do domestic dogs understand
707 human actions as goal-directed? *PLoS ONE*, 9(9), e106530.
708 <https://doi.org/10.1371/journal.pone.0106530>

- 709 Ostojić, L., Legg, E. W., Dits, A., Williams, N., Brecht, K. F., Mendl, M., & Clayton, N. S.
710 (2016a). Experimenter Expectancy Bias Does Not Explain Eurasian Jays' (*Garrulus*
711 *glandarius*) Performance in a Desire-State Attribution Task. *Journal of Comparative*
712 *Psychology*. <https://doi.org/10.1037/com0000043>
- 713 Ostojić, L., Cheke, L. G., Shaw, R. C., Legg, E. W., & Clayton, N. S. (2016b). Desire-state
714 attribution: benefits of a novel paradigm using the food-sharing behavior of Eurasian
715 jays (*Garrulus glandarius*). *Communicative & Integrative Biology*, 9(2), e1134065.
716 <https://doi.org/10.1080/19420889.2015.1134065>
- 717 Ostojić, L., Legg, E. W., Shaw, R. C., Cheke, L. G., Mendl, M., & Clayton, N. S. (2014). Can
718 male Eurasian jays disengage from their own current desire to feed the female what she
719 wants? *Biology Letters*, 10(3), 20140042. <https://doi.org/10.1098/rsbl.2014.0042>
- 720 Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that
721 desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the*
722 *National Academy of Sciences of the United States of America*, 110(10), 4123–4128.
723 <https://doi.org/10.1073/pnas.1209926110>
- 724 Prétôt, L., Weiss, D. J., & Brosnan, S. F. (2018). Do nonhuman primates ascribe goals to the
725 choices of conspecifics? *Animal Behavior and Cognition*, 5, 41-54.
726 <https://doi.org/10.26451/abc.05.01.04.2018>
- 727 Shaw, R. C., MacKinley, R. D., Clayton, N. S., & Burns, K. C. (2017). Male New Zealand
728 robins (*Petroica longipes*) cater to their mate's desire when sharing food in the wild.
729 *Scientific Reports*, 7(1), 896. <https://doi.org/10.1038/s41598-017-00879-1>
- 730 Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2012). A 21 word solition. Retrieved from
731 http://papers.ssrn.com/sol3/papers.cfm?abstract_id=2160588.
732 <https://doi.org/10.2139/ssrn.2160588>
- 733 Simonsohn, U. (2015). Small telescopes: detectability and the evaluation of replication

734 results. *Psychological Science*, 26, 559-560. <https://doi.org/10.1177/0956797614567341>

735 Skelhorn, J., & Rowe, C. (2006). Avian predators taste–reject aposematic prey on the basis of

736 their chemical defence. *Biology Letters*, 2(3), 348–350.

737 <https://doi.org/10.1098/rsbl.2006.0483>

738 Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing:

739 timing and currency of benefits. *Animal Behaviour*, 67(4), 603-614.

740 <https://doi.org/10.1016/j.anbehav.2003.04.012>

741 Vahed, K. (1998). The function of nuptial feeding in insects: a review of empirical studies.

742 *Biological Reviews of the Cambridge Philosophical Society*, 73(01), 43-78.

743 Wood, J. N., Glynn, D. D., Phillips, B. C., & Hauser, M. D. (2007). The perception of

744 rational, goal–directed action in nonhuman primates. *Science*, 317(5843), 1402-1405.

745 <https://doi.org/10.1126.science.1144663>

746 Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach.

747 *Cognition*, 69, 1-34.

748 Woodward, A. L. (1999). Infants' ability to distinguish between purposeful and non-

749 purposeful behaviors. *Infant Behavior and Development*, 22, 145-160.

750