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Food sharing and social cognition

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1   # Food Sharing and Social Cognition

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3   ## Abstract

4   Many non-human animals share food with each other, with kin, mates and other unrelated
5   individuals. When an individual shares food with another they lose a valuable resource. Thus,
6   traditionally much research has investigated how this behaviour can be an evolutionarily stable
7   strategy. Only recently has food sharing behaviour been exploited to investigate non-human
8   cognition. Certain evolutionarily stable strategies that have been proposed as accounts for food
9   sharing behaviours, such as reciprocity and interchange, may rely on complex cognitive abilities.
10   In these cases, an individual may calculate the benefit they may receive from sharing with the
11   recipient. In some species, sharing of food can facilitate the recipients' rate and extent of
12   learning. This form of teaching may be cognitively complex if the donor takes into account the
13   level of the recipient's abilities. In addition, an animal's food sharing behaviour, which in itself
14   may be based on a simple cognitive mechanism, could be used as a tool to investigate the extent
15   to which the individual may be capable of complex cognitive abilities, for example, mental state
16   attribution. These three areas of research: reciprocity, teaching and mental state attribution,
17   illustrate how food-sharing behaviour can be used as a valuable natural behaviour to investigate
18   cognition in non-human animals.

19   ## Introduction

20   Food sharing is a particularly amenable behaviour for investigating the social cognition of non-
21   human animals because it tends to be a distinctly social behaviour and can be observed in a
22   variety of species from insects to primates[1,2]. Food sharing in non-human animals can take active
23   or passive forms. Active forms of food sharing involve the donor performing an action that
24   provisions the recipient with a food item that the donor currently possesses. In primates active
25   sharing can involve the 'handing' of food from one individual to another and in birds active
26   sharing involves the passing of food between individuals' beaks. In contrast, passive forms of
27   food sharing involve the non-monopolisation of a food source because an individual does not
28   defend the food. Thus, passive forms of food sharing include 'tolerated theft' where a donor
29   does not interfere when the recipient attempts to obtain food that is close by the donor[3].

30   Although there are cases where passive sharing may not be distinctly social the majority of the
31   primate food sharing literature combines passive and active forms of sharing and we will use
32   food sharing to refer to both these forms.

33   Traditionally research has focused on the ultimate explanation of food sharing, namely, how this
34   behaviour can be part of an evolutionary stable strategy[4,5]. In line with these ultimate
35   explanations researchers have sought to understand the proximate mechanisms, including the
36   psychological processes, which underlie these strategies. Some researchers claim that certain
37   ultimate explanations of food sharing would require complex cognitive abilities[6,7]. As a
38   consequence, food sharing behaviour has tended to be used for investigating only those
39   psychological processes that have been directly implicated in producing an evolutionary stable
40   strategy.

41   We suggest that there is also a second way in which the food sharing behaviours can be used to
42   test the cognitive mechanisms employed by non-human animals. Experimental techniques that
43   employ natural behaviours are important because the animals are highly motivated to perform
44   these behaviours and because they allow researchers to investigate particular cognitive
45   mechanisms in ecologically valid contexts. Consequently, even if an individual's food sharing
46   behaviour does not have cognitively complex underpinnings this behaviour can still be used as a
47   tool to investigate aspects of cognition that are not directly related to food sharing. Thus, food
48   sharing can be used in a similar way to how the imprinting of juvenile domestic chickens has
49   been used to investigate their numerical and physical cognition[8,9].

50   In this review we will discuss two cases in which food sharing behaviour may be directly reliant
51   on sophisticated cognitive processes, namely reciprocity and teaching. We will then discuss
52   recent research that has used food sharing behaviour as a tool to investigate mental state
53   attribution.

Reciprocity

55   Reciprocity is an ultimate explanation of an animal's food sharing behaviour. It suggests that an
56   evolutionary stable strategy occurs because an individual can gain future benefits from sharing
57   either because they receive these benefits in kind (*reciprocity*[5]) or in another commodity
58   (*interchange*[10,11]). Other benefits may accrue if sharing is used to indicate an individual's own
59   fitness or status to the donor and observers (*costly signalling*[12]). These three types of future benefits
60   are a consequence of the food sharing behaviour influencing an unrelated individual's behaviour
61   and could all be described as a form of reciprocity, albeit in the case of costly signalling in an
62   indirect sense[13]. It should be noted that reciprocity describes one possible evolutionary stable
63   strategy of food sharing and that as such it is ambivalent about the proximate mechanisms
64   underlying the strategy.

65   Patterns of reciprocity (as an ultimate explanation) have been noted in a number of different
66   food sharing species. For instance, the amount of blood shared by vampire bats (*Desmodus*
67   *rotundus*), which share blood with individuals that have failed to forage, is correlated with the
68   amount of blood they have previously received from the recipient[14,15]. Moreover, the largest body
69   of research on food sharing and reciprocity has been conducted on chimpanzees; whose sharing

70 behaviour has been hypothesised to be returned as increased coalitionary support[16,17], increased
71 grooming[18–20] or increased copulations with the recipient[21,22].

72 However, evidence supporting these hypotheses in chimpanzees appears to vary depending on
73 the commodity reciprocated and the study population. Early observations on the chimpanzees at
74 Gombe indicated that males tended to share more with females in oestrous, suggesting that food
75 sharing may yield an immediate reproductive benefit[21,22]. Although a study on a captive
76 population of chimpanzees found that food sharing was correlated with copulations made in the
77 time period surrounding the food sharing event[23], recent work in Gombe and other wild
78 populations found no evidence for this 'meat for sex' hypothesis when considering short term
79 benefits[16,24,25]. This contrasts with evidence supporting the 'food for grooming' hypothesis,
80 because males share more with individuals that have recently groomed them[19,20]. There is
81 evidence that long term benefits for food sharing can come from receiving increased copulations
82 or from increased affiliative behaviours such as grooming[26–28]. For instance, a study on
83 chimpanzees in the Taï forest found that food sharing was correlated with the number of
84 copulations made by a dyad within the 22 month period of the study[26]. Thus, benefits that
85 chimpanzees receive from food sharing may occur in the form of both short and long term
86 interchanges and the timescale of the interchange may vary depending on the commodity.

87 However, it should also be noted that despite the correlations between commodities exchanged
88 these studies may not satisfy the criterion for reciprocity because the correlations could be the
89 result of a third factor. For instance, a field study by Gilby[24] revealed a link between grooming
90 and food sharing on a superficial level. Critically, this link was mediated by harassment; females
91 that had groomed a male gained more food and harassed him at greater frequencies than females
92 that had not groomed him. Consequently, this pattern of behaviour does not satisfy the criterion
93 for reciprocity, Moreover, from a proximate perspective the temporal contiguity between the
94 sharing event and the benefit make it plausible that this behaviour could be learnt through
95 instrumental conditioning (the lack of temporal contiguity in actual cases of reciprocity make this
96 a less plausible explanation of the animals behaviour)[29].

97 The requirement for reciprocity (as an ultimate explanation) to involve a behaviour that brings
98 no immediate evolutionary benefit to an individual is often, mistakenly, considered to mean that
99 the proximate mechanism behind such behaviour must necessarily take into account this future
100 benefit[30–32]. Of the three main hypothesised proximate mechanisms that can account for
101 reciprocity and interchange only one of them requires individuals to take into account the future
102 benefit of their behaviour, namely calculated reciprocity. In the following sections we will discuss
103 the cognitive requirements of the three proximate mechanisms that have been hypothesised to
104 underlie reciprocity before turning to the evidence for these proximate mechanisms.

105 **Calculated Reciprocity**

106 Calculated reciprocity accounts for an animal performing a costly action, such as food sharing,
107 on the basis of calculating the future benefit of that action[18]. From a psychological perspective
108 this mechanism presents the most cognitively demanding explanation of reciprocity[33,34].

109 Calculation of future benefits are thought to require the individual to resist temporal discounting
110 so that the individual does not misrepresent the value of the future reward[6,7]. In addition

111   individuals would need to be able to quantify the commodities reciprocated in order to assess
112   their debt and credit to other individuals[2]. The set of cognitive abilities required for calculated
113   reciprocity has been argued to make it unlikely that this proximate mechanism accounts for many
114   food sharing behaviours[7].

Attitudinal Reciprocity

116   Attitudinal reciprocity suggests that individuals are likely to share more with individuals who they
117   have a positive attitude towards. This attitude is influenced by previous positive and negative
118   interactions with specific individuals[35,36]. Notably because attitudinal reciprocity does not entail
119   representing the value of a future benefit there is no need for a donor to resist temporal
120   discounting. It has also been argued that the attitudinal view reduces the memory load on an
121   individual because they do not have to encode the precise nature of their interactions with an
122   individual because this is quantified by a change in attitude[34].

124   However, there remains an open-question over the time-scale over which the 'attitude' that
125   influences reciprocity operates. One school of thought implies that these attitudes only operate
126   over a short scale of time and would at most take into account the last few interactions between
127   the donor and the recipient[34,35,37]. A second school of thought suggests that these attitudes
128   accumulate over a large time period based on multiple interactions and that for familiar
129   individuals recent negative interactions may be overridden by the accumulation of previous
130   positive ones[32].

Symmetry based reciprocity

132   An even simpler proximate mechanism behind reciprocal food sharing suggests that an
133   individual randomly distributes food to other individuals (regardless of previous interactions)[18].
134   This will eventually lead to each individual performing similar amounts of food sharing with each
135   other if they are within a closed group. However, this *symmetry-based reciprocity*[18] is prone to being
136   infiltrated by cheats who take advantage of this propensity and is unlikely to have evolved as an
137   evolutionary stable strategy[32].

Generalized reciprocity

139   Generalised reciprocity suggests that animals are more likely to share food if they have had a
140   positive interaction with any other individual regardless of who the recipient is. Whereas
141   symmetry based reciprocity is likely to be limited to closed groups *generalised reciprocity* can account
142   for reciprocity within open groups in which individuals are mobile and can move between
143   groups[38]. Models suggest that such reciprocity can occur if individuals tend to perform positive
144   behaviours after any individual has performed a positive behaviour toward them and if the
145   individuals can 'walk away' from a group in some cases where they have not experienced a
146   positive behaviour. Critically, this leads to groups breaking up if there is an influx of cheats,
147   ensuring that there tends to be reciprocation within the group. This kind of reciprocity is reliant
148   on minimal cognitive requirements as it does not necessitate individual recognition because the
149   identity of the donor is irrelevant to which member of the group receives a positive action from
150   the recipient in return[39].

151 **Evidence for the proximate mechanisms**

152 Evidence demonstrating specific proximate mechanisms behind reciprocal food sharing is
153 sparse. In part this is due to research focusing on the ultimate mechanisms of food sharing
154 behaviour. Thus, although there are a number of studies that show correlations indicating a
155 reciprocal pattern of exchange, these studies cannot reveal the proximate mechanism underlying
156 this reciprocation.

157 Attitudinal reciprocity, at least in its short term form as proposed by de Waal[35,36] is thought to be
158 characterised by co-fluctuations in the amount of food shared by individuals in a dyad over a
159 short time period. This co-fluctuation of food exchange is predicted because if an individual is
160 taking into account the immediate previous interactions of an individual they will start to reduce
161 the amount they share when that individual reduced the amount they shared. Evidence of such
162 short term co-fluctuations in sharing behaviour have been shown in capuchin monkeys' and
163 bonobos' food sharing behaviour while longer term correlations have been shown in vampire
164 bats and chimpanzees[15,27,35].

165 Few studies have claimed to demonstrate calculated reciprocity. A notable exception is the result
166 of an orang-utan token exchange task. Dufour et al (2009)[40] suggested that calculated reciprocity
167 could be shown by demonstrating that a donor shares items that are valuable to the recipient but
168 not to themselves and that the donor adapts their sharing behaviour based on the recipients
169 sharing behaviour. Notably, generous donors should share less when the recipient tends to
170 transfer items infrequently and a donor that is initially less generous than the recipient should
171 increase their rate of sharing to maintain high levels of transfer with the recipient. Consequently,
172 two orang-utans who had been trained to exchange tokens with a human in return for food were
173 positioned in two adjacent cages and were able to exchange tokens between each other and with
174 the experimenter. In the critical stages of the experiment 24 tokens were placed in each
175 compartment, all 24 of the tokens were valueless to the occupant of the compartment but 12 of
176 the tokens could be exchanged by the orang-utan in the adjacent compartment for food. In the
177 initial series of trials one individual shared more items than the other individual. However, in
178 subsequent trials the rate of transfers converged and there were correlations between the number
179 of valuable items shared and received in all but the very first session. Furthermore, these
180 exchanges were characterised by turn-taking between the individuals.

181 However, it should be apparent that the results of the orang-utan token exchange experiment
182 could also be achieved if attitudinal reciprocity or generalised reciprocity was being employed.
183 The convergence of each individual's rate of sharing may be explained by changes in attitude or
184 overall tendency to share (as predicted by generalised reciprocity) induced by the lower or higher
185 rate of the other individuals sharing. The correlations found in all but the first session
186 demonstrate co-fluctuations in the amount individual's share – an effect that has been taken as
187 evidence of attitudinal reciprocity. Moreover, the other result that the authors claim indicates
188 calculated reciprocity, namely turn taking, has also been noted in other forms of exchange and in
189 these cases is not thought to involve complex cognition[41]. It is also unclear what to make of the
190 turn-taking behaviour of this single dyad because without the ability to investigate partner choice
191 generalised reciprocity is difficult to rule out. Moreover, other studies have failed to find such
192 turn taking in orang-utans[42].

193   Furthermore, co-fluctuation in sharing behaviours need not be explained by attitudinal
194   reciprocity or calculated reciprocity. Instead this pattern could be the result of an external factor
195   that exerts the same influence on the food sharing behaviour of each individual within a dyad.
196   For instance, if the amount of food shared by an individual is linked to light levels or time of day
197   then because both individuals are exposed to this same factor the quantities that they share are
198   likely to fluctuate. Moreover, absence of such co-fluctuation may be the result of the longer term
199   form of attitudinal reciprocity where a recent negative or positive interaction with an individual
200   may have minimal influence on the emotional score they have gained from other interactions[32].

201   **Future directions**

202   Current research that investigates fluctuations in sharing behaviour without actively manipulating
203   an individual's rate of sharing cannot easily distinguish between the three major proximate
204   mechanisms of reciprocity. Symmetrical reciprocity makes a clear prediction that an individual's
205   own rate of sharing should not be influenced by a recipient's rate of sharing. As such
206   experimental manipulations of the recipient's rate of sharing should not influence the donor's
207   rate of sharing and if these rates do vary then the subject is engaging in either attitudinal or
208   calculated reciprocity. Note that relying on natural variations in the rates of sharing gives rise to
209   the possibility that both individuals' rates of sharing are influenced by an external variable.

210   A harder task is to foresee where the predictions of the sharing behaviours expected from
211   attitudinal and calculated reciprocity diverge. We see two possible ways in which such a
212   distinction could be made. Firstly, attitudinal reciprocity should be immune to the constraints
213   imposed on calculated sharing by the need to resist temporal discounting. Secondly, calculated
214   reciprocity should be immune to any experimental manipulations of the subject's attitude toward
215   an individual. Until studies begin to manipulate these constraints it remains impossible to
216   definitively demonstrate that reciprocal food sharing behaviours are based on anything other
217   than symmetrical reciprocity.

218   **Teaching**

219   Teaching in non-human species is typically considered on a functional rather than a mechanistic
220   basis[43,44]. Therefore, evidence of teaching need not implicate the sophisticated cognitive
221   mechanisms that can underlie human pedagogy[45,46]. Reflecting this approach Caro and Hauser's[43]
222   commonly cited definition of teaching in non-human animals is concerned with i) whether an
223   actor modifies their behaviour in the presence of a naïve individual (at a cost to themselves), ii)
224   whether this modification exerts an influence on the naïve individual, and iii) whether this results
225   either in the naïve individual learning a new skill or influences the rate or efficiency with which
226   the naïve individual acquires the skill[43]. Although there are a limited number of examples of
227   teaching in the wild a large proportion of these examples involve parents sharing food with their
228   offspring. Parent-offspring food sharing may be a particularly fruitful context for investigating
229   teaching behaviours because sharing food with naïve infants can provide them with the
230   opportunity to learn about *what* is edible and *how* certain, difficult-to-handle, foods can be
231   accessed[47,48].

232   Food sharing has been proposed to increase the breadth of infant's knowledge about which food
233   is edible[49] Within primates the callitrichids, a family that includes tamarins and marmosets, are

234 atypical because of the large quantity of food infants obtain from parental sharing behaviour.
235 However, tests of the function of callitrichid food sharing behaviour have produced mixed
236 results. One study on Tamarins has showed that they increased the amount of novel foods they
237 shared with infants and one study has not found this effect[50,51]. Moreover, a study on common
238 marmosets (*Callithrix jacchus*) that manipulated the novelty and palatability of food items found
239 that parents did not facilitate the dietary choices of their infants by selectively exposing them to
240 novel food items and that parents actually shared unpalatable novel food with the infants at the
241 highest rate[52].

242 Despite the lack of evidence that food sharing can add to *what* infants know to be edible there is
243 evidence that food sharing can allow infants to gain skills about *how* to access or obtain difficult-
244 to-handle food. Animals can acquire skills through observing the products of another's actions,
245 either because the actions have made the task easier or because the effect draws attention to a
246 key stimulus[53,54]. There is evidence that this form of teaching may occur in some carnivorous
247 species with parents releasing dead or maimed prey for their infants to hunt – this might provide
248 the opportunity for the infants to hone their hunting skills. For instance, there is anecdotal
249 evidence that raptors such as ospreys (*Pandion haliaetus*) display this type of behaviour, by
250 dropping fish for their young to catch. Moreover, observational studies on felids indicate that
251 they release prey to offspring and that experimentally provisioning prey to the kittens of
252 domestic cats (*Felis silvestris catus*) improves their ability to hunt[55–58]. There is also strong evidence
253 of this behaviour in meerkats, which we will return to later[59].

254 A further example of a behaviour that satisfies the functional definition of teaching has been
255 observed in the pied babbler (*Turdoides bicolor*). During parent-offspring food sharing bouts
256 babblers produce purr calls. These calls are costly because parents that produce a greater number
257 of purr calls have reduced weight; unlike in other species the calls do not increase the efficiency
258 of the sharing bout[60]. Importantly, the frequency of these food calls increases as the chicks near
259 fledging age. The contingency between calls and shared food has the effect of conditioning the
260 chicks to associate these calls with food[60]. These food calls are then used by the parents in the
261 post-fledging period to recruit their young to novel foraging locations[61]. Thus, unlike the other
262 forms of food sharing discussed here, which provide infants with experience about a particular
263 food, food sharing in pied babblers provides infants with the opportunity to learn an association
264 between their parents' purr call and the presence of food.

265 These food sharing behaviours can also be experimentally tested to investigate which cognitive
266 mechanisms may underlie the teaching behaviour. Theoretically distinguishing cognitively
267 demanding teaching from less cognitively demanding teaching has proven controversial and this
268 is partly due to questions about what constitutes teaching in humans[44,45]. For the purpose of this
269 review we distinguish between *ability based teaching* and *harmonised teaching* (note that these terms
270 are not typically used within the literature but offer an apt description of the proximate
271 mechanisms behind teaching in non-human animals).

272 **Ability Based Teaching**

273 *Ability based teaching* requires the tutor to alter the type of food they share with their pupil based
274 on the pupils ability. Critically, teachers should be able to detect deficiencies in the pupil's ability

275 and make steps to alter their behaviour appropriately[46]. Thus, even if a tutor's behaviour is
276 primarily reliant on a single cue that indicates their pupil's ability they should be able to detect
277 deficiencies from other cues. Byrne and Rappaport (2011)[46] give an example in which a school
278 teacher starts giving a lesson to a class based on the average knowledge of like-aged pupils
279 without gauging the abilities of individual students but if necessary the teacher can still recognise
280 if a student is struggling and adjust their teaching appropriately.

281 From a cognitive perspective this level of sensitivity to a pupil's ability requires recognising how
282 well another individual can perform an action. Moreover, in cases where teaching aims to
283 increase a pupil's knowledge, such as increasing their dietary breadth, it would be necessary for
284 the tutor to keep track of what the pupil has or has not had experience of. In cases where
285 teaching aims to increase a pupil's physical ability tutors may need to recognise the intentions
286 behind the pupil's failed actions. Evidence for such abilities outside of the context of teaching
287 would appear to be limited to certain primates and corvids[62–64].

288 **Harmonised Teaching**

289 In *harmonised teaching* a teacher's behaviour maps onto a pupil's changing ability because of
290 stereotyped responses to a single cue. For instance, Caro and Hauser (1992) suggest that teaching
291 could occur if a mother altered her behaviour in a stereotyped time course that was dependent
292 on her own hormonal changes from birth. Critically, *harmonised teaching* can be distinguished from
293 *ability based teaching* because it relies on a stereotyped response to a single cue which could lead to
294 mothers mistakenly changing their teaching behaviour if this cue was not in line with their pupil's
295 ability, an effect that is unlikely to occur in *ability based teaching.*

296 Outside of the food sharing context this form of teaching has been shown in ants, which are
297 unlikely to possess the cognitive mechanisms necessary for ability based teaching. These ants run
298 in tandem toward a food source and a knowledgeable leader will wait for a naïve follower. This
299 behaviour is likely to be a result of a hard-wired slowing response when the leader is at a certain
300 distance from the follower[65].

301 **Evidence for the proximate mechanisms of teaching**

302 Evidence of teaching via food sharing behaviour is relatively rare and the precise mechanism
303 behind such behaviours has only been investigated in detail in one species, meerkats[59].

304 Meerkats are cooperative breeders, and tend to form groups of around 15 individuals with the
305 dominant pair being the primary reproducers[66,67]. Food is shared with infants by conspecific
306 helpers[68]. The shared food tends to consist of invertebrates and the quantity of the food shared
307 is linked to the offspring's life time reproductive success[69]. A significant proportion of an adult
308 meerkat's diet consists of scorpions that contain potent neurotoxins and scorpions that
309 aggressively defend themselves[70]. These scorpions are also shared with offspring and helpers
310 typically provision dead scorpions or scorpions with the sting removed[59]. Critically, the frequency
311 with which dead or disabled scorpions are shared with infants decreases with the age of the
312 infant. Experimental manipulations of the type of scorpions provided to offspring indicate that
313 infant meerkats who had previously received live scorpions to handle are more successful or
314 faster at handling scorpions than infants that had previously received dead scorpions or infants

315 that had received a quantity of boiled egg equivalent in weight to the scorpions provided to the
316 other infants.

317 Critically, the changes in the items shared with infants are mediated by changes to the infants'
318 begging calls, for instance, when auditory playbacks of older infants are played within a group
319 that has young infants helpers provision a greater proportion of intact scorpions than after
320 hearing playbacks of young infants[59]. The results of the auditory playbacks indicate that the
321 meerkats are likely to be showing a hard-wired response to the infants' begging calls rather than
322 considering the infants' actual abilities which implicates harmonised teaching.

323 **Future directions**

324 Important questions remain about which cognitive mechanisms can explain the teaching
325 behaviour of animals. Teaching in humans often requires a sensitivity to the level of the pupil's
326 knowledge and ability[71]. It has been suggested that such sensitivity does not underlie meerkats'
327 teaching behaviour because they respond stereotypically to auditory playbacks of infants' begging
328 calls. However, these playbacks were conducted in a single experimental session and if the
329 helpers primarily rely on auditory information about the infants' abilities then this stereotyped
330 response is unsurprising because they had limited opportunity to receive feedback that their
331 primary indicator of the infants' ability was incorrect. Consequently, it would be important to
332 establish whether helpers adjust their sharing behaviour when they are repeatedly presented with
333 auditory information that conflicts with the infants' actual ability. If the meerkats are sensitive to
334 the infants' ability then under these cases of repeated exposure the helpers should adjust their
335 sharing behaviour. A similar test is required to establish whether pied babblers are sensitive to
336 their infants' ability to pair the purr call with receiving food. Infants that have learnt that
337 receiving food and purr calls are associated beg more when purr calls are played. If parents are
338 sensitive to how well the chicks have learnt the contingency then they should modulate the
339 frequency with which they pair calls and food sharing based on the chicks begging behaviour to
340 their purr calls.

341 These studies suggest that food sharing behaviour can play an important role in the transmission
342 of information between generations. However, due to the limited number of experiments
343 indicating teaching behaviour in non-human animals and the uncertainty surrounding the
344 mechanisms that underlie each of these abilities further experiments are necessary to establish
345 the cognitive mechanisms that underpin the use of food sharing as a form of teaching.

346 **Mental State Attribution**

347 One of the questions raised by evidence of teaching in non-human animals is whether or not the
348 teachers are sensitive to their pupil's knowledge. Sensitivity to others' knowledge is part of a
349 special form of social cognition concerned with the attribution of internal mental states to
350 others, namely Theory of Mind[72,73]. Humans are able to accurately predict another's actions by
351 attributing mental states such as beliefs and desires to them. Critically, Theory of Mind would
352 require animals to distinguish their own mental states from another's (self-other differentiation)
353 and to account for the representational nature of these mental states (beliefs represent reality,
354 desires represent the desired outcome). Food sharing can be used to investigate these factors
355 because many species are motivated to share high quality food, i.e. food that the donor desires.

356 Self-other differentiation can be tested by investigating whether donors can cater to the desires
357 of a recipient that differ to their own desire. Moreover, a donor's ability to account for the
358 representational nature of desires can be tested by investigating whether they can account for the
359 differences in two individuals' desires or changes to the same individual's desire. However, in
360 non-human animals, distinguishing the ability to attribute mental states from a simpler cognitive
361 mechanism has proven difficult. Critically, mental states cannot be directly observed but must
362 instead be inferred from observations of behaviours or situations that cause particular mental
363 states or deduced from observing the effect of a mental state[74]. Consequently, research cannot
364 easily distinguish cases in which an animal attributes a mental state from cases in which the
365 animal responds to the behaviour of an individual without attributing a mental state (behaviour
366 reading)[75,76]. Different forms of behaviour reading could explain an animal's ability to share
367 desirable food with a recipient. For instance, a donor may share if the recipient is begging for
368 food. Critically, the donor need not attribute a desire to recognise that he should share in this
369 context. Thus, tests of Theory of Mind on non-human animals must not only test for self-other
370 differentiation and the ability to account for the representational nature of mental states, they
371 must also control and rule out behaviour reading as an alternative explanation [77,78]. The food
372 sharing behaviour of non-human animals allows for these alternative explanations to be
373 empirically investigated by manipulating the donor's and recipient's desires and the way in which
374 donors are informed of the recipient's desire[79]. To date the only research that exploits the food
375 sharing behaviour in the context of Theory of Mind has been conducted on corvids.

376 **Desire State Attribution: Eurasian jays**

377 During their breeding season male Eurasian jays (*Garralus glandarius*) actively share high quality
378 food with their female partners. This behaviour has been used to investigate whether the male
379 jay can share food that is in line with the female's current desire as manipulated through specific
380 satiety. Specific satiety refers to the devaluation for a particular food after being sated on it[80–82].
381 In the first study that investigated the cognitive mechanism behind the male's sharing behaviour,
382 the male was fed on the jays' maintenance diet (MD), while he saw his female partner being fed
383 on either MD, wax moth larvae (W) or mealworm beetle larvae (M). These three conditions were
384 run on separate days. This meant that when the female had been fed on MD her desire was
385 neutral, whereas when she had been fed W she had a greater desire for M and when she had
386 been prefed M she had a greater desire for W. In the subsequent test phase, the male was given
387 20 choices between a single W or M which he could choose to eat, cache or share with the
388 female. The larvae types the male chose to share were in line with his partner's desire: he shared
389 a higher proportion of W when she was sated on M than when she was sated on W[83], indicating
390 that the male Eurasian jay catered for his partner's desire.

391 Furthermore, two alternative explanations of this result have been ruled out. The first is that the
392 male did not differentiate between his own desire and his partner's desire, i.e. that he did not
393 demonstrate self-other differentiation. This explanation suggests that the male changed the food
394 he shared with his partner because his own desire for the two food types was influenced by
395 having watched his partner eat one food type to satiety. However, when the male was not able to
396 share, the food he ate did not vary based on what the female had eaten. Thus the female's desire
397 did not influence the male's own desire for the foods. The second alternative explanation of the
398 male's behaviour is that he used a behavioural indication at the time of sharing to respond to the

399 female's desire. Such a direct response to a behaviour would be considered a form of 'stimulus
400 bound behaviour reading'[76]. However, the male's use of behavioural indications at the time of
401 sharing was ruled out by an experiment in which the female was fed out of sight of the male such
402 that he did not know what she was sated on. Here, the only way in which the male could cater
403 for his partner's desire was if he relied on some form of indication of her desire. The results
404 showed that the male was unable to do so, suggesting that the male's sharing behaviour was not
405 a result of 'stimulus bound behaviour reading'.

406 A further study, in which both the male's and female's desires were manipulated by specific
407 satiety, has investigated whether the male jay can disengage from his own desire to cater for his
408 partner's desire[84]. In this experiment the desire of the male was manipulated by sating him on
409 either W or M and the female's desire either matched the male's own desire (e.g. she was sated
410 on W when he was sated on W: *matched condition*), was neutral (she was fed MD on both days:
411 *neutral condition*) or was in conflict with the male's own desire (e.g. she was sated on W when he
412 was sated on M: *conflicting condition*). Although the male could disengage from his own desire to
413 cater for his partner's conflicting desire, his response was biased in comparison to the matched
414 and neutral conditions. Critically, this result reflects studies of biases on adult humans' Theory of
415 Mind which provide evidence that adults' judgements of others' motivations are biased by their
416 own motivational state[85]. There is further evidence that adults make more errors when judging
417 another person's belief that differs to their own than when making equivalent judgements about
418 their own memory or when following an arbitrary rule[86,87]. Thus, evidence that the male jay is
419 biased by his own current desire state when catering for his partner's desire state indicates that a
420 similar process may govern the attribution of mental states in Eurasian jays and humans.

421

Future directions

423 These studies present a novel way of testing mental state attribution through the use of food
424 sharing and by manipulating the donor's and recipient's desires. While the current findings rule
425 out the possibility that the male jay relies on 'stimulus bound behaviour reading', further tests are
426 necessary to test for other behaviour reading explanations of the jay's behaviour. The male's
427 behaviour could be based on him having observed a particular behaviour exhibited by his partner
428 during the feeding phase of the experiment, for instance the male might be reliant on observing
429 his partner reject the food that she is sated on[88]. This could be tested by comparing the male's
430 response to their partner's food rejection behaviour with their response when the female is given
431 just enough food to be sated such that she rejects no food at all. It would also be possible to
432 present a scenario where the male does not actually see his partner's eating behaviour but instead
433 has to infer what his partner has eaten from seeing what food was initially provided to her[89]. A
434 further way of alleviating behaviour reading explanations is to demonstrate the flexibility of the
435 individual's response. While the hypothetical experiments described above would demonstrate
436 that the male responds to disparate cues indicating his partner's desire they are both reliant on
437 specific satiety. Thus, an important test of the cognitive mechanism behind the jays' food sharing
438 behaviour would be to demonstrate that the males can cater for their partner's desire in
439 circumstances other than those induced through specific satiety. For instance, if a male observed
440 a female choosing to eat a single W over a single M, would he attribute that she desired W (note

441 that this attribution is in the opposite direction to the effect of specific satiety where the female
442 eating multiple W would lead to her desiring M)? In addition, the food sharing behaviour of
443 other species could be used to investigate whether desire attribution in this context is only
444 exhibited by Eurasian jays, or whether the ability is present in other large brained birds such as
445 corvids and parrots, and whether food- sharing primates also possess this ability.

446 It may also prove possible to use the food sharing behaviours of primates in a similar manner. A
447 recent study showed that capuchin monkeys protected their food more after seeing another
448 eating[90]. Whether this result is a consequence of capuchin's food protection behaviours being
449 triggered after observing another's eating behaviour or a more sophisticated ability remains to be
450 tested.

451 ## Conclusions

452 This review has discussed whether there is any evidence linking the food sharing behaviour of
453 non-human animals with complex cognitive abilities. Critically, we have discussed evidence that
454 food sharing behaviour may or may not be (i) beneficial to the donor, (ii) important for
455 recipients' learning, and (iii) based on the attribution of desires to the recipient. However, it is
456 clear that currently there is limited empirical evidence linking specific cognitive mechanisms with
457 these outcomes and that further research is necessary to better establish the cognitive
458 foundations of these behaviours. This future research will complement the large body of
459 research that has considered the ultimate mechanisms behind food sharing.

460 The fact that complex cognition may not underlie food sharing itself should not put researchers
461 off using this behaviour as a tool for investigating complex cognitive abilities. Just as imprinting
462 has been used to investigate the cognitive abilities of domestic chickens[8,9], food sharing could be
463 used to investigate the cognitive abilities of a wide variety of animals. The use of the Eurasian
464 jays' food sharing behaviour to investigate whether they attribute mental states reflects such an
465 approach. Future experiments on other species could investigate other sophisticated cognitive
466 abilities For example, if a species has a sharing patterns that follows a specific order, such as
467 rooks[91], which only share with subordinate conspecifics, it would be possible to test whether
468 individuals are surprised by sharing events that happen in the wrong direction and whether they
469 can use transitive inference to recognise a novel conspecific's position in the hierarchy[92]. In
470 summary, current studies have only touched the surface of what could be investigated using the
471 food sharing behaviour of non-human animals and further exploitation of this behaviour might
472 produce important insights into non-human cognition.

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