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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 donor³.

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3 30 Although there are cases where passive sharing may not be distinctly social the majority of the
4 31 primate food sharing literature combines passive and active forms of sharing and we will use
5 32 food sharing to refer to both these forms.

7 33 Traditionally research has focused on the ultimate explanation of food sharing, namely, how this
8 34 behaviour can be part of an evolutionary stable strategy^{4,5}. In line with these ultimate
9 35 explanations researchers have sought to understand the proximate mechanisms, including the
10 36 psychological processes, which underlie these strategies. Some researchers claim that certain
11 37 ultimate explanations of food sharing would require complex cognitive abilities^{6,7}. As a
12 38 consequence, food sharing behaviour has tended to be used for investigating only those
13 39 psychological processes that have been directly implicated in producing an evolutionary stable
14 40 strategy.

17 41 We suggest that there is also a second way in which the food sharing behaviours can be used to
18 42 test the cognitive mechanisms employed by non-human animals. Experimental techniques that
19 43 employ natural behaviours are important because the animals are highly motivated to perform
20 44 these behaviours and because they allow researchers to investigate particular cognitive
21 45 mechanisms in ecologically valid contexts. Consequently, even if an individual's food sharing
22 46 behaviour does not have cognitively complex underpinnings this behaviour can still be used as a
23 47 tool to investigate aspects of cognition that are not directly related to food sharing. Thus, food
24 48 sharing can be used in a similar way to how the imprinting of juvenile domestic chickens has
25 49 been used to investigate their numerical and physical cognition^{8,9}.

28 50 In this review we will discuss two cases in which food sharing behaviour may be directly reliant
29 51 on sophisticated cognitive processes, namely reciprocity and teaching. We will then discuss
30 52 recent research that has used food sharing behaviour as a tool to investigate mental state
31 53 attribution.

36 54 **Reciprocity**

37 55 Reciprocity is an ultimate explanation of an animal's food sharing behaviour. It suggests that an
38 56 evolutionary stable strategy occurs because an individual can gain future benefits from sharing
39 57 either because they receive these benefits in kind (*reciprocity*⁵) or in another commodity
40 58 (*interchange*^{10,11}). Other benefits may accrue if sharing is used to indicate an individual's own
41 59 fitness or status to the donor and observers (*costly signalling*¹²). These three types of future benefits
42 60 are a consequence of the food sharing behaviour influencing an unrelated individual's behaviour
43 61 and could all be described as a form of reciprocity, albeit in the case of costly signalling in an
44 62 indirect sense¹³. It should be noted that reciprocity describes one possible evolutionary stable
45 63 strategy of food sharing and that as such it is ambivalent about the proximate mechanisms
46 64 underlying the strategy.

51 65 Patterns of reciprocity (as an ultimate explanation) have been noted in a number of different
52 66 food sharing species. For instance, the amount of blood shared by vampire bats (*Desmodus*
53 67 *rotundus*), which share blood with individuals that have failed to forage, is correlated with the
54 68 amount of blood they have previously received from the recipient^{14,15}. Moreover, the largest body
55 69 of research on food sharing and reciprocity has been conducted on chimpanzees; whose sharing

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3 70 behaviour has been hypothesised to be returned as increased coalitionary support^{16,17}, increased
4 71 grooming^{18–20} or increased copulations with the recipient^{21,22}.

6 72 However, evidence supporting these hypotheses in chimpanzees appears to vary depending on
7 73 the commodity reciprocated and the study population. Early observations on the chimpanzees at
8 74 Gombe indicated that males tended to share more with females in oestrous, suggesting that food
9 75 sharing may yield an immediate reproductive benefit^{21,22}. Although a study on a captive
10 76 population of chimpanzees found that food sharing was correlated with copulations made in the
11 77 time period surrounding the food sharing event²³, recent work in Gombe and other wild
12 78 populations found no evidence for this ‘meat for sex’ hypothesis when considering short term
13 79 benefits^{16,24,25}. This contrasts with evidence supporting the ‘food for grooming’ hypothesis,
14 80 because males share more with individuals that have recently groomed them^{19,20}. There is
15 81 evidence that long term benefits for food sharing can come from receiving increased copulations
16 82 or from increased affiliative behaviours such as grooming^{26–28}. For instance, a study on
17 83 chimpanzees in the Tai forest found that food sharing was correlated with the number of
18 84 copulations made by a dyad within the 22 month period of the study²⁶. Thus, benefits that
19 85 chimpanzees receive from food sharing may occur in the form of both short and long term
20 86 interchanges and the timescale of the interchange may vary depending on the commodity.

25 87 However, it should also be noted that despite the correlations between commodities exchanged
26 88 these studies may not satisfy the criterion for reciprocity because the correlations could be the
27 89 result of a third factor. For instance, a field study by Gilby²⁴ revealed a link between grooming
28 90 and food sharing on a superficial level. Critically, this link was mediated by harassment; females
29 91 that had groomed a male gained more food and harassed him at greater frequencies than females
30 92 that had not groomed him. Consequently, this pattern of behaviour does not satisfy the criterion
31 93 for reciprocity. Moreover, from a proximate perspective the temporal contiguity between the
32 94 sharing event and the benefit make it plausible that this behaviour could be learnt through
33 95 instrumental conditioning (the lack of temporal contiguity in actual cases of reciprocity make this
34 96 a less plausible explanation of the animals behaviour)²⁹.

37 97 The requirement for reciprocity (as an ultimate explanation) to involve a behaviour that brings
38 98 no immediate evolutionary benefit to an individual is often, mistakenly, considered to mean that
39 99 the proximate mechanism behind such behaviour must necessarily take into account this future
40 100 benefit^{30–32}. Of the three main hypothesised proximate mechanisms that can account for
41 101 reciprocity and interchange only one of them requires individuals to take into account the future
42 102 benefit of their behaviour, namely calculated reciprocity. In the following sections we will discuss
43 103 the cognitive requirements of the three proximate mechanisms that have been hypothesised to
44 104 underlie reciprocity before turning to the evidence for these proximate mechanisms.

50 105 **Calculated Reciprocity**

51 106 Calculated reciprocity accounts for an animal performing a costly action, such as food sharing,
52 107 on the basis of calculating the future benefit of that action¹⁸. From a psychological perspective
53 108 this mechanism presents the most cognitively demanding explanation of reciprocity^{33,34}.

54 109 Calculation of future benefits are thought to require the individual to resist temporal discounting
55 110 so that the individual does not misrepresent the value of the future reward^{6,7}. In addition
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3 111 individuals would need to be able to quantify the commodities reciprocated in order to assess
4 112 their debt and credit to other individuals². The set of cognitive abilities required for calculated
5 113 reciprocity has been argued to make it unlikely that this proximate mechanism accounts for many
6 114 food sharing behaviours⁷.

8 9 115 **Attitudinal Reciprocity**

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11 116 Attitudinal reciprocity suggests that individuals are likely to share more with individuals who they
12 117 have a positive attitude towards. This attitude is influenced by previous positive and negative
13 118 interactions with specific individuals^{35,36}. Notably because attitudinal reciprocity does not entail
14 119 representing the value of a future benefit there is no need for a donor to resist temporal
15 120 discounting. It has also been argued that the attitudinal view reduces the memory load on an
16 121 individual because they do not have to encode the precise nature of their interactions with an
17 122 individual because this is quantified by a change in attitude³⁴.

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20 124 However, there remains an open-question over the time-scale over which the ‘attitude’ that
21 125 influences reciprocity operates. One school of thought implies that these attitudes only operate
22 126 over a short scale of time and would at most take into account the last few interactions between
23 127 the donor and the recipient^{34,35,37}. A second school of thought suggests that these attitudes
24 128 accumulate over a large time period based on multiple interactions and that for familiar
25 129 individuals recent negative interactions may be overridden by the accumulation of previous
26 130 positive ones³².

27 28 29 30 131 **Symmetry based reciprocity**

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32 132 An even simpler proximate mechanism behind reciprocal food sharing suggests that an
33 133 individual randomly distributes food to other individuals (regardless of previous interactions)¹⁸.
34 134 This will eventually lead to each individual performing similar amounts of food sharing with each
35 135 other if they are within a closed group. However, this *symmetry-based reciprocity*¹⁸ is prone to being
36 136 infiltrated by cheats who take advantage of this propensity and is unlikely to have evolved as an
37 137 evolutionary stable strategy³².

38 39 40 138 **Generalized reciprocity**

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42 139 Generalised reciprocity suggests that animals are more likely to share food if they have had a
43 140 positive interaction with any other individual regardless of who the recipient is. Whereas
44 141 symmetry based reciprocity is likely to be limited to closed groups *generalised reciprocity* can account
45 142 for reciprocity within open groups in which individuals are mobile and can move between
46 143 groups³⁸. Models suggest that such reciprocity can occur if individuals tend to perform positive
47 144 behaviours after any individual has performed a positive behaviour toward them and if the
48 145 individuals can ‘walk away’ from a group in some cases where they have not experienced a
49 146 positive behaviour. Critically, this leads to groups breaking up if there is an influx of cheats,
50 147 ensuring that there tends to be reciprocation within the group. This kind of reciprocity is reliant
51 148 on minimal cognitive requirements as it does not necessitate individual recognition because the
52 149 identity of the donor is irrelevant to which member of the group receives a positive action from
53 150 the recipient in return³⁹.

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3 151 **Evidence for the proximate mechanisms**
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5 152 Evidence demonstrating specific proximate mechanisms behind reciprocal food sharing is
6 153 sparse. In part this is due to research focusing on the ultimate mechanisms of food sharing
7 154 behaviour. Thus, although there are a number of studies that show correlations indicating a
8 155 reciprocal pattern of exchange, these studies cannot reveal the proximate mechanism underlying
9 156 this reciprocation.

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12 157 Attitudinal reciprocity, at least in its short term form as proposed by de Waal^{35,36} is thought to be
13 158 characterised by co-fluctuations in the amount of food shared by individuals in a dyad over a
14 159 short time period. This co-fluctuation of food exchange is predicted because if an individual is
15 160 taking into account the immediate previous interactions of an individual they will start to reduce
16 161 the amount they share when that individual reduced the amount they shared. Evidence of such
17 162 short term co-fluctuations in sharing behaviour have been shown in capuchin monkeys' and
18 163 bonobos' food sharing behaviour while longer term correlations have been shown in vampire
19 164 bats and chimpanzees^{15,27,35}.

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23 165 Few studies have claimed to demonstrate calculated reciprocity. A notable exception is the result
24 166 of an orang-utan token exchange task. Dufour et al (2009)⁴⁰ suggested that calculated reciprocity
25 167 could be shown by demonstrating that a donor shares items that are valuable to the recipient but
26 168 not to themselves and that the donor adapts their sharing behaviour based on the recipients
27 169 sharing behaviour. Notably, generous donors should share less when the recipient tends to
28 170 transfer items infrequently and a donor that is initially less generous than the recipient should
29 171 increase their rate of sharing to maintain high levels of transfer with the recipient. Consequently,
30 172 two orang-utans who had been trained to exchange tokens with a human in return for food were
31 173 positioned in two adjacent cages and were able to exchange tokens between each other and with
32 174 the experimenter. In the critical stages of the experiment 24 tokens were placed in each
33 175 compartment, all 24 of the tokens were valueless to the occupant of the compartment but 12 of
34 176 the tokens could be exchanged by the orang-utan in the adjacent compartment for food. In the
35 177 initial series of trials one individual shared more items than the other individual. However, in
36 178 subsequent trials the rate of transfers converged and there were correlations between the number
37 179 of valuable items shared and received in all but the very first session. Furthermore, these
38 180 exchanges were characterised by turn-taking between the individuals.

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43 181 However, it should be apparent that the results of the orang-utan token exchange experiment
44 182 could also be achieved if attitudinal reciprocity or generalised reciprocity was being employed.
45 183 The convergence of each individual's rate of sharing may be explained by changes in attitude or
46 184 overall tendency to share (as predicted by generalised reciprocity) induced by the lower or higher
47 185 rate of the other individuals sharing. The correlations found in all but the first session
48 186 demonstrate co-fluctuations in the amount individual's share – an effect that has been taken as
49 187 evidence of attitudinal reciprocity. Moreover, the other result that the authors claim indicates
50 188 calculated reciprocity, namely turn taking, has also been noted in other forms of exchange and in
51 189 these cases is not thought to involve complex cognition⁴¹. It is also unclear what to make of the
52 190 turn-taking behaviour of this single dyad because without the ability to investigate partner choice
53 191 generalised reciprocity is difficult to rule out. Moreover, other studies have failed to find such
54 192 turn taking in orang-utans⁴².

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3 193 Furthermore, co-fluctuation in sharing behaviours need not be explained by attitudinal
4 194 reciprocity or calculated reciprocity. Instead this pattern could be the result of an external factor
5 195 that exerts the same influence on the food sharing behaviour of each individual within a dyad.
6
7 196 For instance, if the amount of food shared by an individual is linked to light levels or time of day
8 197 then because both individuals are exposed to this same factor the quantities that they share are
9 198 likely to fluctuate. Moreover, absence of such co-fluctuation may be the result of the longer term
10 199 form of attitudinal reciprocity where a recent negative or positive interaction with an individual
11 200 may have minimal influence on the emotional score they have gained from other interactions³².

13 201 **Future directions**

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16 202 Current research that investigates fluctuations in sharing behaviour without actively manipulating
17 203 an individual's rate of sharing cannot easily distinguish between the three major proximate
18 204 mechanisms of reciprocity. Symmetrical reciprocity makes a clear prediction that an individual's
19 205 own rate of sharing should not be influenced by a recipient's rate of sharing. As such
20 206 experimental manipulations of the recipient's rate of sharing should not influence the donor's
21 207 rate of sharing and if these rates do vary then the subject is engaging in either attitudinal or
22 208 calculated reciprocity. Note that relying on natural variations in the rates of sharing gives rise to
23 209 the possibility that both individuals' rates of sharing are influenced by an external variable.

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27 210 A harder task is to foresee where the predictions of the sharing behaviours expected from
28 211 attitudinal and calculated reciprocity diverge. We see two possible ways in which such a
29 212 distinction could be made. Firstly, attitudinal reciprocity should be immune to the constraints
30 213 imposed on calculated sharing by the need to resist temporal discounting. Secondly, calculated
31 214 reciprocity should be immune to any experimental manipulations of the subject's attitude toward
32 215 an individual. Until studies begin to manipulate these constraints it remains impossible to
33 216 definitively demonstrate that reciprocal food sharing behaviours are based on anything other
34 217 than symmetrical reciprocity.

35 36 37 218 **Teaching**

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40 219 Teaching in non-human species is typically considered on a functional rather than a mechanistic
41 220 basis^{43,44}. Therefore, evidence of teaching need not implicate the sophisticated cognitive
42 221 mechanisms that can underlie human pedagogy^{45,46}. Reflecting this approach Caro and Hauser's⁴³
43 222 commonly cited definition of teaching in non-human animals is concerned with i) whether an
44 223 actor modifies their behaviour in the presence of a naïve individual (at a cost to themselves), ii)
45 224 whether this modification exerts an influence on the naïve individual, and iii) whether this results
46 225 either in the naïve individual learning a new skill or influences the rate or efficiency with which
47 226 the naïve individual acquires the skill⁴⁵. Although there are a limited number of examples of
48 227 teaching in the wild a large proportion of these examples involve parents sharing food with their
49 228 offspring. Parent-offspring food sharing may be a particularly fruitful context for investigating
50 229 teaching behaviours because sharing food with naïve infants can provide them with the
51 230 opportunity to learn about *what* is edible and *how* certain, difficult-to-handle, foods can be
52 231 accessed^{47,48}.

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57 232 Food sharing has been proposed to increase the breadth of infant's knowledge about which food
58 233 is edible⁴⁹ 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 rate⁵².

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 later⁵⁹.

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 bout⁶⁰. 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 food⁶⁰. These food calls are then used by the parents in the
261 post-fledging period to recruit their young to novel foraging locations⁶¹. 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

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3 275 and make steps to alter their behaviour appropriately⁴⁶. Thus, even if a tutor's behaviour is
4 276 primarily reliant on a single cue that indicates their pupil's ability they should be able to detect
5 277 deficiencies from other cues. Byrne and Rappaport (2011)⁴⁶ give an example in which a school
6 278 teacher starts giving a lesson to a class based on the average knowledge of like-aged pupils
7 279 without gauging the abilities of individual students but if necessary the teacher can still recognise
8 280 if a student is struggling and adjust their teaching appropriately.

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11 281 From a cognitive perspective this level of sensitivity to a pupil's ability requires recognising how
12 282 well another individual can perform an action. Moreover, in cases where teaching aims to
13 283 increase a pupil's knowledge, such as increasing their dietary breadth, it would be necessary for
14 284 the tutor to keep track of what the pupil has or has not had experience of. In cases where
15 285 teaching aims to increase a pupil's physical ability tutors may need to recognise the intentions
16 286 behind the pupil's failed actions. Evidence for such abilities outside of the context of teaching
17 287 would appear to be limited to certain primates and corvids⁶²⁻⁶⁴.

20 21 288 **Harmonised Teaching**

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23 289 In *harmonised teaching* a teacher's behaviour maps onto a pupil's changing ability because of
24 290 stereotyped responses to a single cue. For instance, Caro and Hauser (1992) suggest that teaching
25 291 could occur if a mother altered her behaviour in a stereotyped time course that was dependent
26 292 on her own hormonal changes from birth. Critically, *harmonised teaching* can be distinguished from
27 293 *ability based teaching* because it relies on a stereotyped response to a single cue which could lead to
28 294 mothers mistakenly changing their teaching behaviour if this cue was not in line with their pupil's
29 295 ability, an effect that is unlikely to occur in *ability based teaching*.

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32 296 Outside of the food sharing context this form of teaching has been shown in ants, which are
33 297 unlikely to possess the cognitive mechanisms necessary for ability based teaching. These ants run
34 298 in tandem toward a food source and a knowledgeable leader will wait for a naïve follower. This
35 299 behaviour is likely to be a result of a hard-wired slowing response when the leader is at a certain
36 300 distance from the follower⁶⁵.

37 38 39 301 **Evidence for the proximate mechanisms of teaching**

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41 302 Evidence of teaching via food sharing behaviour is relatively rare and the precise mechanism
42 303 behind such behaviours has only been investigated in detail in one species, meerkats⁵⁹.

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45 304 Meerkats are cooperative breeders, and tend to form groups of around 15 individuals with the
46 305 dominant pair being the primary reproducers^{66,67}. Food is shared with infants by conspecific
47 306 helpers⁶⁸. The shared food tends to consist of invertebrates and the quantity of the food shared
48 307 is linked to the offspring's life time reproductive success⁶⁹. A significant proportion of an adult
49 308 meerkat's diet consists of scorpions that contain potent neurotoxins and scorpions that
50 309 aggressively defend themselves⁷⁰. These scorpions are also shared with offspring and helpers
51 310 typically provision dead scorpions or scorpions with the sting removed⁵⁹. Critically, the frequency
52 311 with which dead or disabled scorpions are shared with infants decreases with the age of the
53 312 infant. Experimental manipulations of the type of scorpions provided to offspring indicate that
54 313 infant meerkats who had previously received live scorpions to handle are more successful or
55 314 faster at handling scorpions than infants that had previously received dead scorpions or infants

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3 315 that had received a quantity of boiled egg equivalent in weight to the scorpions provided to the
4 316 other infants.

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6 317 Critically, the changes in the items shared with infants are mediated by changes to the infants'
7 318 begging calls, for instance, when auditory playbacks of older infants are played within a group
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9 319 that has young infants helpers provision a greater proportion of intact scorpions than after
10 320 hearing playbacks of young infants⁵⁹. The results of the auditory playbacks indicate that the
11 321 meerkats are likely to be showing a hard-wired response to the infants' begging calls rather than
12 322 considering the infants' actual abilities which implicates harmonised teaching.

14 323 **Future directions**

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16 324 Important questions remain about which cognitive mechanisms can explain the teaching
17 325 behaviour of animals. Teaching in humans often requires a sensitivity to the level of the pupil's
18 326 knowledge and ability⁷¹. It has been suggested that such sensitivity does not underlie meerkats'
19 327 teaching behaviour because they respond stereotypically to auditory playbacks of infants' begging
20 328 calls. However, these playbacks were conducted in a single experimental session and if the
21 329 helpers primarily rely on auditory information about the infants' abilities then this stereotyped
22 330 response is unsurprising because they had limited opportunity to receive feedback that their
23 331 primary indicator of the infants' ability was incorrect. Consequently, it would be important to
24 332 establish whether helpers adjust their sharing behaviour when they are repeatedly presented with
25 333 auditory information that conflicts with the infants' actual ability. If the meerkats are sensitive to
26 334 the infants' ability then under these cases of repeated exposure the helpers should adjust their
27 335 sharing behaviour. A similar test is required to establish whether pied babblers are sensitive to
28 336 their infants' ability to pair the purr call with receiving food. Infants that have learnt that
29 337 receiving food and purr calls are associated beg more when purr calls are played. If parents are
30 338 sensitive to how well the chicks have learnt the contingency then they should modulate the
31 339 frequency with which they pair calls and food sharing based on the chicks begging behaviour to
32 340 their purr calls.

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38 341 These studies suggest that food sharing behaviour can play an important role in the transmission
39 342 of information between generations. However, due to the limited number of experiments
40 343 indicating teaching behaviour in non-human animals and the uncertainty surrounding the
41 344 mechanisms that underlie each of these abilities further experiments are necessary to establish
42 345 the cognitive mechanisms that underpin the use of food sharing as a form of teaching.

44 346 **Mental State Attribution**

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47 347 One of the questions raised by evidence of teaching in non-human animals is whether or not the
48 348 teachers are sensitive to their pupil's knowledge. Sensitivity to others' knowledge is part of a
49 349 special form of social cognition concerned with the attribution of internal mental states to
50 350 others, namely Theory of Mind^{72,73}. Humans are able to accurately predict another's actions by
51 351 attributing mental states such as beliefs and desires to them. Critically, Theory of Mind would
52 352 require animals to distinguish their own mental states from another's (self-other differentiation)
53 353 and to account for the representational nature of these mental states (beliefs represent reality,
54 354 desires represent the desired outcome). Food sharing can be used to investigate these factors
55 355 because many species are motivated to share high quality food, i.e. food that the donor desires.

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3 356 Self-other differentiation can be tested by investigating whether donors can cater to the desires
4 357 of a recipient that differ to their own desire. Moreover, a donor's ability to account for the
5 358 representational nature of desires can be tested by investigating whether they can account for the
6 359 differences in two individuals' desires or changes to the same individual's desire. However, in
7 360 non-human animals, distinguishing the ability to attribute mental states from a simpler cognitive
8 361 mechanism has proven difficult. Critically, mental states cannot be directly observed but must
9 362 instead be inferred from observations of behaviours or situations that cause particular mental
10 363 states or deduced from observing the effect of a mental state⁷⁴. Consequently, research cannot
11 364 easily distinguish cases in which an animal attributes a mental state from cases in which the
12 365 animal responds to the behaviour of an individual without attributing a mental state (behaviour
13 366 reading)^{75,76}. Different forms of behaviour reading could explain an animal's ability to share
14 367 desirable food with a recipient. For instance, a donor may share if the recipient is begging for
15 368 food. Critically, the donor need not attribute a desire to recognise that he should share in this
16 369 context. Thus, tests of Theory of Mind on non-human animals must not only test for self-other
17 370 differentiation and the ability to account for the representational nature of mental states, they
18 371 must also control and rule out behaviour reading as an alternative explanation^{77,78}. The food
19 372 sharing behaviour of non-human animals allows for these alternative explanations to be
20 373 empirically investigated by manipulating the donor's and recipient's desires and the way in which
21 374 donors are informed of the recipient's desire⁷⁹. To date the only research that exploits the food
22 375 sharing behaviour in the context of Theory of Mind has been conducted on corvids.

23 376 **Desire State Attribution: Eurasian jays**

24 377 During their breeding season male Eurasian jays (*Garrulus glandarius*) actively share high quality
25 378 food with their female partners. This behaviour has been used to investigate whether the male
26 379 jay can share food that is in line with the female's current desire as manipulated through specific
27 380 satiety. Specific satiety refers to the devaluation for a particular food after being sated on it⁸⁰⁻⁸².
28 381 In the first study that investigated the cognitive mechanism behind the male's sharing behaviour,
29 382 the male was fed on the jays' maintenance diet (MD), while he saw his female partner being fed
30 383 on either MD, wax moth larvae (W) or mealworm beetle larvae (M). These three conditions were
31 384 run on separate days. This meant that when the female had been fed on MD her desire was
32 385 neutral, whereas when she had been fed W she had a greater desire for M and when she had
33 386 been preferred M she had a greater desire for W. In the subsequent test phase, the male was given
34 387 20 choices between a single W or M which he could choose to eat, cache or share with the
35 388 female. The larvae types the male chose to share were in line with his partner's desire: he shared
36 389 a higher proportion of W when she was sated on M than when she was sated on W⁸³, indicating
37 390 that the male Eurasian jay catered for his partner's desire.

38 391 Furthermore, two alternative explanations of this result have been ruled out. The first is that the
39 392 male did not differentiate between his own desire and his partner's desire, i.e. that he did not
40 393 demonstrate self-other differentiation. This explanation suggests that the male changed the food
41 394 he shared with his partner because his own desire for the two food types was influenced by
42 395 having watched his partner eat one food type to satiety. However, when the male was not able to
43 396 share, the food he ate did not vary based on what the female had eaten. Thus the female's desire
44 397 did not influence the male's own desire for the foods. The second alternative explanation of the
45 398 male's behaviour is that he used a behavioural indication at the time of sharing to respond to the
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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 desire⁸⁴. 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 state⁸⁵. 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

422 **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 on⁸⁸. 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 her⁸⁹. 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

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3 441 that this attribution is in the opposite direction to the effect of specific satiety where the female
4 442 eating multiple W would lead to her desiring M)? In addition, the food sharing behaviour of
5 443 other species could be used to investigate whether desire attribution in this context is only
6 444 exhibited by Eurasian jays, or whether the ability is present in other large brained birds such as
7 445 corvids and parrots, and whether food-sharing primates also possess this ability.

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10 446 It may also prove possible to use the food sharing behaviours of primates in a similar manner. A
11 447 recent study showed that capuchin monkeys protected their food more after seeing another
12 448 eating⁹⁰. Whether this result is a consequence of capuchin's food protection behaviours being
13 449 triggered after observing another's eating behaviour or a more sophisticated ability remains to be
14 450 tested.

15 16 17 451 **Conclusions**

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19 452 This review has discussed whether there is any evidence linking the food sharing behaviour of
20 453 non-human animals with complex cognitive abilities. Critically, we have discussed evidence that
21 454 food sharing behaviour may or may not be (i) beneficial to the donor, (ii) important for
22 455 recipients' learning, and (iii) based on the attribution of desires to the recipient. However, it is
23 456 clear that currently there is limited empirical evidence linking specific cognitive mechanisms with
24 457 these outcomes and that further research is necessary to better establish the cognitive
25 458 foundations of these behaviours. This future research will complement the large body of
26 459 research that has considered the ultimate mechanisms behind food sharing.

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30 460 The fact that complex cognition may not underlie food sharing itself should not put researchers
31 461 off using this behaviour as a tool for investigating complex cognitive abilities. Just as imprinting
32 462 has been used to investigate the cognitive abilities of domestic chickens^{8,9}, food sharing could be
33 463 used to investigate the cognitive abilities of a wide variety of animals. The use of the Eurasian
34 464 jays' food sharing behaviour to investigate whether they attribute mental states reflects such an
35 465 approach. Future experiments on other species could investigate other sophisticated cognitive
36 466 abilities. For example, if a species has a sharing patterns that follows a specific order, such as
37 467 rooks⁹¹, which only share with subordinate conspecifics, it would be possible to test whether
38 468 individuals are surprised by sharing events that happen in the wrong direction and whether they
39 469 can use transitive inference to recognise a novel conspecific's position in the hierarchy⁹². In
40 470 summary, current studies have only touched the surface of what could be investigated using the
41 471 food sharing behaviour of non-human animals and further exploitation of this behaviour might
42 472 produce important insights into non-human cognition.

43 44 45 46 47 473 **References**

- 48
49
50 474 1. Vahed K. The function of nuptial feeding in insects: a review of empirical studies. *Biol Rev*
51 475 *Camb Philos Soc.* 1998;73(01):43–78.
- 52
53 476 2. Stevens JR, Gilby IC. A conceptual framework for nonkin food sharing: timing and
54 477 currency of benefits. *Anim Behav.* 2004;67(4):603–614. doi:10.1016/j.anbehav.2003.04.012.
- 55
56 478 3. Blurton Jones NG. A selfish origin for human food sharing: Tolerated theft. *Ethol*
57 479 *Sociobiol.* 1984;5(1):1–3. doi:10.1016/0162-3095(84)90030-X.
- 58
59
60

- 1
2
3 480 4. Hamilton W. The genetical evolution of social behaviour. I. *J Theor Biol.* 1964.
4
5 481 5. Trivers RL. The Evolution of Reciprocal Altruism. *Q Rev Biol.* 1971;46(1):35–57.
6
7 482 6. Stevens JR, Cushman F a., Hauser MD. Evolving the Psychological Mechanisms for
8 483 Cooperation. *Annu Rev Ecol Evol Syst.* 2005;36(1):499–518.
9 484 doi:10.1146/annurev.ecolsys.36.113004.083814.
10
11
12 485 7. Stevens JR, Hauser MD. Why be nice? Psychological constraints on the evolution of
13 486 cooperation Why be nice? Psychological constraints on the evolution of cooperation.
14 487 *Trends Cogn Sci.* 2004;8(2):60–5. doi:10.1016/j.tics.2003.12.003.
15
16 488 8. Chiandetti C, Vallortigara G. Intuitive physical reasoning about occluded objects by
17 489 inexperienced chicks. *Proc Biol Sci.* 2011;278(1718):2621–7. doi:10.1098/rspb.2010.2381.
18
19
20 490 9. Rugani R, Regolin L, Vallortigara G. Rudimental numerical competence in 5-day-old
21 491 domestic chicks (*Gallus gallus*): identification of ordinal position. *J Exp Psychol Anim Behav*
22 492 *Process.* 2007;33(1):21–31. doi:10.1037/0097-7403.33.1.21.
23
24 493 10. Hemelrijk CK. A Matrix Partial Correlation Test used in Investigations of Reciprocity and
25 494 Other Social Interaction Patterns at Group Level. 1990.
26
27 495 11. Hemelrijk CK, Ek A. Reciprocity and interchange of grooming and “support” in captive
28 496 chimpanzees. *Anim Behav.* 1991;41(6):923–935. doi:10.1016/S0003-3472(05)80630-X.
29
30 497 12. Zahavi A. Reliability in communication systems and the evolution of altruism. In:
31 498 Stonehouse B, Perrins CM, eds. *Evolutionary Ecology*. London: Macmillan Press; 1977:253–
32 499 260.
33
34
35 500 13. Nowak M a, Sigmund K. Evolution of indirect reciprocity. *Nature.* 2005;437(7063):1291–
36 501 8. doi:10.1038/nature04131.
37
38 502 14. Wilkinson G. Reciprocal food sharing in the vampire bat. *Nature.* 1984.
39
40 503 15. Carter GG, Wilkinson GS. Food sharing in vampire bats: reciprocal help predicts
41 504 donations more than relatedness or harassment. *Proc R Soc B Biol Sci.* 2013;280.
42
43 505 16. Mitani JC, Watts DP. Why do chimpanzees hunt and share meat? 2001;(Stanford
44 506 1998):915–924. doi:10.1006/anbe.2000.1681.
45
46
47 507 17. Nishida T, Hasegawa T. Meat-sharing as a coalition strategy by an alpha male chimpanzee.
48 508 *Top Primatol.* 1992;1:159–174.
49
50 509 18. de Waal FBM, Luttrell LM. Mechanisms of Social Reciprocity in Three Primate Species:
51 510 Symmetrical Relationship Characteristics or Cognition? *Ethol Sociobiol.* 1988;9:101–118.
52
53 511 19. de Waal FBM. The chimpanzee’s service economy: Food for grooming. *Evol Hum Behav.*
54 512 1997;18:375–386.
55
56
57 513 20. de Waal FBM. Food sharing and reciprocal obligations among chimpanzees. *J Hum Evol.*
58 514 1989;18:433–459.
59
60

- 1
2
3 515 21. Stanford C. *Chimpanzee and red colobus: the ecology of predator and prey*. Cranbury, New Jersey:
4 516 Associated University Press; 1998.
- 5
6 517 22. Teleki G. *The predatory behavior of wild chimpanzees*. Cambridge, MA: Harvard University
7 518 Press; 1973.
- 8
9
10 519 23. Crick J, Suchak M, Eppley TM. The roles of food quality and sex in chimpanzee sharing
11 520 behavior (*Pan troglodytes*). 2013;150:1203–1224. doi:10.1163/1568539X-00003087.
- 12
13 521 24. Gilby IC. Meat sharing among the Gombe chimpanzees: harassment and reciprocal
14 522 exchange. *Anim Behav*. 2006;71(4):953–963. doi:10.1016/j.anbehav.2005.09.009.
- 15
16 523 25. Gilby IC, Emery Thompson M, Ruane JD, Wrangham R. No evidence of short-term
17 524 exchange of meat for sex among chimpanzees. *J Hum Evol*. 2010;59(1):44–53.
18 525 doi:10.1016/j.jhevol.2010.02.006.
- 19
20 526 26. Gomes CM, Boesch C. Wild Chimpanzees Exchange Meat for Sex on a Long- Term
21 527 Basis. *PLoS One*. 2009;4(4):16–18. doi:10.1371/journal.pone.0005116.
- 22
23
24 528 27. Jaeggi A V, Groot E De, Stevens JMG, Schaik CP Van. Evolution and Human Behavior
25 529 Mechanisms of reciprocity in primates: testing for short-term contingency of grooming
26 530 and food sharing in bonobos and chimpanzees. *Evol Hum Behav*. 2013;34(2):69–77.
27 531 doi:10.1016/j.evolhumbehav.2012.09.005.
- 28
29 532 28. Muller MN, Mitani JC. Conflict and Cooperation in Wild Chimpanzees. *Adv Study Behav*.
30 533 2005;35:276–331. doi:10.1016/S0065-3454(05)35007-8.
- 31
32 534 29. Rescorla RA, Holland PC. Behavioral Studies of Associative Learning in Animals. *Annu*
33 535 *Rev Psychol*. 1982;33(1):265–308. doi:10.1146/annurev.ps.33.020182.001405.
- 34
35
36 536 30. Schino G, Aureli F. A few misunderstandings about reciprocal altruism. *Commun Integr*
37 537 *Biol*. 2010;3(6):561–3. doi:10.4161/cib.3.6.12977.
- 38
39 538 31. West S a, Griffin a S, Gardner a. Social semantics: altruism, cooperation, mutualism,
40 539 strong reciprocity and group selection. *J Evol Biol*. 2007;20(2):415–32. doi:10.1111/j.1420-
41 540 9101.2006.01258.x.
- 42
43 541 32. Schino G, Aureli F, Di I, Tecnolegie SE, Cognizione D. Reciprocal Altruism in
44 542 Primates□ : Partner Choice , Cognition , and Emotions. 2009;39(09):45–69.
45 543 doi:10.1016/S0065-3454(09)39002-6.
- 46
47
48 544 33. Brosnan SF, de Waal FBM. A proximate perspective on reciprocal altruism. *Hum Nat*.
49 545 2002;13(1):129–152.
- 50
51 546 34. De Waal FBM, Brosnan SF. Simple and complex reciprocity in primates. 2005:79–100.
- 52
53 547 35. De Waal FBM. Attitudinal reciprocity in food sharing among brown capuchin monkeys.
54 548 *Anim Behav*. 2000;60:253–261. doi:10.1006/anbe.2000.1471.
- 55
56
57 549 36. De Waal FBM, Suchak M. Prosocial primates: selfish and unselfish motivations. *Philos*
58 550 *Trans R Soc Lond B Biol Sci*. 2010;365(1553):2711–22. doi:10.1098/rstb.2010.0119.
- 59
60

- 1
2
3 551 37. De Waal FBM, Suchak M. Prosocial primates□ : selfish and unselfish motivations
4 552 Prosocial primates□ : selfish and unselfish motivations. 2010;(August).
5 553 doi:10.1098/rstb.2010.0119.
6
7 554 38. Hamilton IM, Taborsky M. Contingent movement and cooperation evolve under
8 555 generalized reciprocity. *Proc Biol Sci.* 2005;272(1578):2259–67.
9 556 doi:10.1098/rspb.2005.3248.
10
11 557 39. Pfeiffer T, Rutte C, Killingback T, Taborsky M, Bonhoeffer S. Evolution of cooperation
12 558 by generalized reciprocity. *Proc Biol Sci.* 2005;272(1568):1115–20.
13 559 doi:10.1098/rspb.2004.2988.
14
15 560 40. Dufour V, Pelé M, Neumann M, Thierry B, Call J. Calculated reciprocity after all□ :
16 561 computation behind token transfers in orang-utans Calculated reciprocity after all□ :
17 562 computation behind token transfers in. 2009;(December 2008).
18 563 doi:10.1098/rsbl.2008.0644.
19
20 564 41. Fischer EA. Mating behavior in the black hamlet — gamete trading or egg trading?
21 565 *Environ Biol Fishes.* 1987;18(2):143–148. doi:10.1007/BF00002602.
22
23 566 42. Pele M, Thierry B. Token Transfers Among Great Apes (Gorilla gorilla , Pongo
24 567 pygmaeus , Pan paniscus , and Pan troglodytes): Species Differences , Gestural Requests ,
25 568 and Reciprocal Exchange. 2009;123(4):375–384. doi:10.1037/a0017253.
26
27 569 43. Caro TM, Hauser MD. Is There Teaching in Nonhuman Animals? *Q Rev Biol.*
28 570 1992;67(2):151–174.
29
30 571 44. Thornton A. Teachers in the wild: some clarification. *Trends Cogn Sci.* 2007;11(7):272–273.
31 572 doi:10.1016/j.tics.2007.05.006.
32
33 573 45. Csibra G. Teachers in the wild. 2007;11(3):95–96. doi:10.1016/j.tics.2006.11.010.
34
35 574 46. Byrne RW, Rapaport LG. What are we learning from teaching? *Anim Behav.*
36 575 2011;82(5):1207–1211. doi:10.1016/j.anbehav.2011.08.018.
37
38 576 47. Rapaport LG, Brown GR. Social influences on foraging behavior in young nonhuman
39 577 primates: Learning what, where, and how to eat. *Evol Anthropol Issues, News, Rev.*
40 578 2008;17(4):189–201. doi:10.1002/evan.20180.
41
42 579 48. Brown GR, Almond REA, van Bergen Y. Begging, stealing and offering: food transfer in
43 580 non-human primates. *Adv Study Behav.* 2004;34:265–295.
44
45 581 49. Ewer R. The behaviour of the meerkat, *Suricata suricatta* (Schreber). *Z Tierpsychol.*
46 582 1963:570–607.
47
48 583 50. Rapaport LG. Provisioning of young in golden lion tamarins (*Callitrichidae*,
49 584 *Leontopithecus rosalia*): a test of the information hypothesis. *Ethology.* 1999;105:619–636.
50
51 585 51. Price E., Feistner AT. Food sharing in lion tamarins: tests of three hypotheses. *Am J*
52 586 *Primatol.* 1993:211–221.
53
54
55
56
57
58
59
60

- 1
2
3 587 52. Brown GR, Almond REA, Bates NJ. Adult-infant food transfer in common marmosets:
4 588 an experimental study. *Am J Primatol.* 2005;65(4):301–12. doi:10.1002/ajp.20117.
- 5
6 589 53. Terkel J. Cultural transmission of feeding behaviour in black rats. In: Heyes CM, Galef
7 590 BG, eds. *Social Learning in Animals The Roots of Culture*. San Diego: Academic Press;
8 591 1996:17–47.
- 9
10 592 54. Galef BG, Giraldeau L-A. Social influences on foraging in vertebrates: causal mechanisms
11 593 and adaptive functions. *Anim Behav.* 2001;61(1):3–15. doi:10.1006/anbe.2000.1557.
- 12
13 594 55. Meinertzhagen R. The education of young ospreys. *Ibis (Lond 1859)*. 1954:153–155.
- 14
15 595 56. Caro TM. Effects of the mother, object play, and adult experience on predation in cats.
16 596 *Behav Neural Biol.* 1980;29(1):29–51.
- 17
18 597 57. Caro TM. The effects of experience on the predatory patterns of cats. *Behav Neural Biol.*
19 598 1980;29(1):1–28.
- 20
21 599 58. Caro TM. Short-term costs and correlates of play in cheetahs. *Anim Behav.*
22 600 1995;49(2):333–345. doi:10.1006/anbe.1995.9999.
- 23
24 601 59. Thornton A, McAuliffe K. Teaching in Wild Meerkats. 2006;313:228–229.
25 602 doi:10.1126/science.1128727.
- 26
27 603 60. Raihani NJ, Ridley AR. Experimental evidence for teaching in wild pied babblers. *Anim*
28 604 *Behav.* 2008;75(1):3–11. doi:10.1016/j.anbehav.2007.07.024.
- 29
30 605 61. Radford AN, Ridley AR. Recruitment calling: a novel form of extended parental care in an
31 606 altricial species. *Curr Biol.* 2006;16(17):1700–1704. doi:10.1016/j.cub.2006.06.053.
- 32
33 607 62. Emery NJ, Clayton NS. Effects of experience and social context on prospective caching
34 608 strategies by scrub jays. *Nature.* 2001;414(6862):443–446. doi:10.1038/35106560.
- 35
36 609 63. Bugnyar T, Heinrich B. Ravens, *Corvus corax*, differentiate between knowledgeable and
37 610 ignorant competitors. *Proc Biol Sci.* 2005;272(1573):1641–1646.
38 611 doi:10.1098/rspb.2005.3144.
- 39
40 612 64. Tomasello M, Call J, Hare B. Chimpanzees understand psychological states – the question
41 613 is which ones and to what extent. *Trends Cogn Sci.* 2003;7(4):153–156. doi:10.1016/S1364-
42 614 6613(03)00035-4.
- 43
44 615 65. Franks NR, Richardson T. Teaching in tandem-running ants. *Nature.* 2006;439(7073):153.
45 616 doi:10.1038/439153a.
- 46
47 617 66. Clutton-Brock TH, Gaynor D, McIlrath GM, et al. Predation, group size and mortality in
48 618 a cooperative mongoose, *Suricata suricatta*. *J Anim Ecol.* 1999;68(4):672–683.
49 619 doi:10.1046/j.1365-2656.1999.00317.x.
- 50
51 620 67. Clutton-Brock TH, Brotherton PN, Russell AF, et al. Cooperation, control, and
52 621 concession in meerkat groups. *Science.* 2001;291(5503):478–481.
- 53
54
55
56
57
58
59
60

- 1
2
3 622 68. Brotherton PNM, Clutton-Brock TH, Riain MJO, et al. Offspring food allocation by
4 623 parents and helpers in a cooperative mammal. *Behav Ecol.* 2001;12(5):590–599.
- 5
6 624 69. Russell A., Young A., Spong G, Jordan N., Clutton-Brock T. Helpers increase the
7 625 reproductive potential of offspring in cooperative meerkats. *Proc R Soc B Biol Sci.*
8 626 2007;274(1609):513–520. doi:10.1098/rspb.2006.3698.
- 9
10 627 70. Doolan S, Macdonald D. Diet and foraging behaviour of group living meerkats, *Suricata*
11 628 *suricatta*, in the southern Kalahari. *J Zool.* 1996;239:697–716.
- 12
13
14 629 71. Strauss S, Ziv M, Stein A. Teaching as a natural cognition and its relations to
15 630 preschoolers' developing theory of mind. *Cogn Dev.* 2002;17(3-4):1473–1487.
16 631 doi:10.1016/S0885-2014(02)00128-4.
- 17
18 632 72. Premack D, Woodruff G. Does the chimpanzee have a theory of mind? *Behav Brain Sci.*
19 633 1978;1(04):515–526. doi:10.1017/S0140525X00076512.
- 20
21 634 73. Frith CD, Frith U. Theory of mind. *Curr Biol.* 2005;15(17):644–645.
- 22
23
24 635 74. Heyes CM. Anecdotes, training, trapping and triangulating: do animals attribute mental
25 636 states? *Anim Behav.* 1993;46:177–188.
- 26
27 637 75. Povinelli DJ, Vonk J. Chimpanzee minds: suspiciously human? *Trends Cogn Sci.*
28 638 2003;7(4):157–160. doi:10.1016/S1364-6613(03)00053-6.
- 29
30 639 76. Penn D, Povinelli DJ. The comparative delusion: the behavioristic/mentalistic dichotomy
31 640 in comparative theory of mind research. In: Metcalfe J, Terrace HS, eds. *Agency and joint*
32 641 *attention.* Vol 3. Oxford: Oxford University Press; 2013:62–81.
33 642 doi:10.1093/acprof:oso/9780199988341.001.0001.
- 34
35
36 643 77. Heyes CM. Theory of mind in nonhuman primates. *Behav Brain Sci.* 1998:101–148.
- 37
38 644 78. Lurz RW. If chimpanzees are mindreaders, could behavioral science tell? Toward a
39 645 solution of the logical problem. *Philos Psychol.* 2009;22(3):305–328.
40 646 doi:10.1080/09515080902970673.
- 41
42 647 79. Ostojic L, Cheke LG, Shaw RC, Legg EW, Clayton NS. Desire-state attribution: Benefits
43 648 of a novel paradigm using the food-sharing behaviour of Eurasian jays (*Garrulus*
44 649 *glandarius*). In Press. *Commun Integr Biol.* 7(1):e34412.
- 45
46
47 650 80. Dickinson A, Balleine B. Motivational control of goal-directed action. *Anim Learn Behav.*
48 651 1994;22(1):1–18. doi:10.3758/BF03199951.
- 49
50 652 81. Dickinson A, Balleine B. Motivational Control of Instrumental Action. *Psychol Sci.*
51 653 1995;4(5):162–167.
- 52
53
54 654 82. Cheke LG, Clayton NS. Eurasian jays (*Garrulus glandarius*) overcome their current
55 655 desires to anticipate two distinct future needs and plan for them appropriately. *Biol Lett.*
56 656 2012;8(2):171–175. doi:10.1098/rsbl.2011.0909.
- 57
58
59
60

- 1
2
3 657 83. Ostojic L, Shaw RC, Cheke LG, Clayton NS. Evidence suggesting that desire-state
4 658 attribution may govern food sharing in Eurasian jays. *Proc Natl Acad Sci U S A*.
5 659 2013;110(10):4123–4128. doi:10.1073/pnas.1209926110.
- 6
7 660 84. Ostojic L, Legg EW, Shaw RC, Cheke LG, Mendl M, Clayton NS. Can male Eurasian jays
8 661 disengage from their current desire to feed the female what she wants? *Biol Lett*. 2014.
- 9
10 662 85. Van Boven L, Loewenstein G. Social projection of transient drive states. *Pers Soc Psychol*
11 663 *Bull*. 2003;29(9):1159–1168. doi:10.1177/0146167203254597.
- 12
13 664 86. Sommerville J a, Bernstein DM, Meltzoff AN. Measuring beliefs in centimeters: private
14 665 knowledge biases preschoolers' and adults' representation of others' beliefs. *Child Dev*.
15 666 2013;84(6):1846–1854. doi:10.1111/cdev.12110.
- 16
17 667 87. Apperly IA, Carroll DJ, Samson D, Humphreys GW, Qureshi A, Moffitt G. Why are
18 668 there limits on theory of mind use? Evidence from adults' ability to follow instructions
19 669 from an ignorant speaker. *Q J Exp Psychol (Hove)*. 2010;63(6):1201–1217.
20 670 doi:10.1080/17470210903281582.
- 21
22 671 88. Kamil AC. Eurasian jays predict the food preferences of their mates. *Proc Natl Acad Sci U*
23 672 *S A*. 2013;110(10):3719–3720. doi:10.1073/pnas.1300515110.
- 24
25 673 89. Taylor AH. Corvid Cognition. *WIREs Cogn Sci*. 2014;5:361–372. doi:10.1002/wcs.1286.
- 26
27 674 90. Hattori Y, Leimgruber K, Fujita K, de Waal FBM. Food-related tolerance in capuchin
28 675 monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-
29 676 consumption. *Behaviour*. 2012;149(2):171–185. doi:10.1163/156853912X634124.
- 30
31 677 91. Scheid C, Schmidt J, Noë R. Distinct patterns of food offering and co-feeding in rooks.
32 678 *Anim Behav*. 2008;76(5):1701–1707. doi:10.1016/j.anbehav.2008.07.023.
- 33
34 679 92. Paz-Y-Miño C G, Bond AB, Kamil AC, Balda RP. Pinyon jays use transitive inference to
35 680 predict social dominance. *Nature*. 2004;430(7001):778–81. doi:10.1038/nature02723.
- 36
37 681
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42 682
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45 683
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