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ANIMAL BEHAVIOUR: ADVANTAGES AND
DISADVANTAGES NO.5

Kevin Brewer

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Orsett Psychological Services
PO Box 179
Grays
Essex
RM16 3EW
UK

orsettpsychologicalservices@phoncoop.coop

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Kevin Brewer BSocSc, MSc
(<http://kmbpsychology.jottit.com/>)

An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

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1. SELFISH GROUP LIVING

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1.1. BENEFITS OF GROUP LIVING

Living in a group (eg: flock, school, herd) gives the individual animal the benefits of safety in numbers. This is manifest in different ways (Goulart and Young 2013):

1. Dilution effect.

Less probability of being predated than alone. The dilution effect has limitations. In other words, the benefits of a group in reducing the individual predation risk does not continue as the group size increases. There is an optimal group size (the risk threshold) where no further benefits are gained for protection from predators, but above that the costs of group living increase (eg: increased conspicuousness of large group and thus increased amount of attacks) (Cresswell and Quinn 2011).

Cresswell and Quinn (2011) described some of the factors relevant to optimal group size:

- Larger groups have increased attack rate because of conspicuousness (selection pressure for smaller groups).
- Increased vigilance from more eyes will rise until it reaches a maximum (eg: 112 pairs of eyes is little better than 111 pairs).
- The individual predation risk ¹ decreases with group size (selection pressure for larger groups).
- Where predators can consume a large number of prey, large groups greater risk (pressure for smaller groups)
- eg: baleen whale consume entire group of krill.

¹ The individual predation risk is influenced by factors like the predator attack rate (which depends on the "encounter effect" - the likelihood of being found by a predator, and this is higher for larger groups), the probability of detecting a predator, and the probability of escaping any attack (which is greater with the dilution effect, unless the predator can consume the whole group) (Roberts 1996).

- Whether the risks are similar for an individual or a group - eg: crossing a crocodile-filled river. In this case, the larger the group, the better for the individual.

What is the optimal group size? Obviously, it varies between species, but here is an example of an attempt to calculate the size of a flock. Cresswell and Quinn (2011) observed daily redshank (*Tringa totanus*) (figure 1.1) flock sizes in East Lothian, Scotland, for 57 days. The main predator is the Eurasian sparrowhawk (*Accipiter nisus*), and their attack rate and success were calculated.



(Source: 4028mdk09)

Figure 1.1 - Redshank.

The redshanks preferred group sizes of between 30-80 individuals, and this appeared to be the optimal range.

The attack rate of the sparrowhawks increased with group size to peak at about 55 individuals, while success declined with increasing group size to even off at groups of 40 individuals.

Cresswell and Quinn (2011) proposed the following equation for overall predation risk for an individual in a group as:

$$\text{Predator attack success} \times \text{attack rate} \times 1/\text{group size}$$

So, for example, using their data:

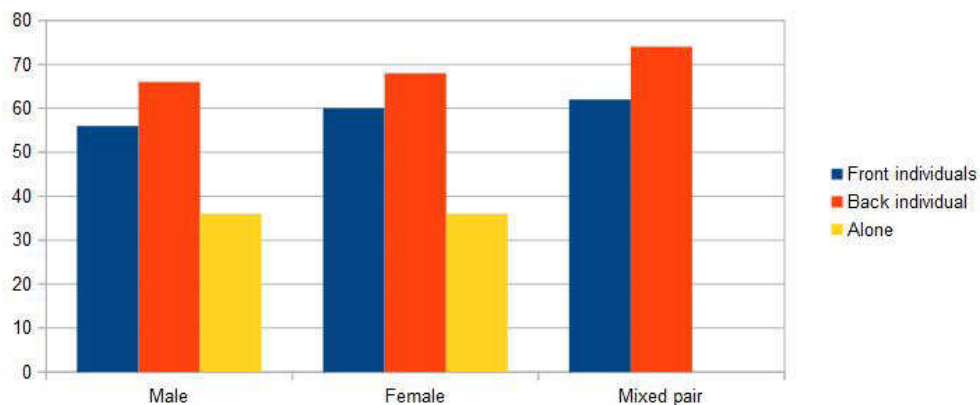
Group of 2	= 0.30 (footnote ²) x 0.5 x 0.5	= 0.075
Group of 10	= 0.20 x 0.75 x 0.1	= 0.015
Group of 40	= 0.10 x 2.0 x 0.025	= 0.005
Alone	= 0.35 x 0.5 x 1	= 0.175

A smaller number is less risk, and so the individual bird is much better off in a group of 40 in this example than in a pair or a group of 10, or alone.

The dilution effect can work as an anti-predator strategy with only a pair of individuals compared to a singleton, as shown by an experiment with termites.

Using the termite, *Reticulitermes chinensis*, Li et al (2013) found that two individuals escaped a predator ant (*Leptogenys kitteli*) more often than an individual. The termites were placed at one end of a tube and had to reach the other end, but inbetween was a single predator. For single termites (male or female), the mean escape rate was 36%. Two termites together (male-male, female-female, or female-male) performed "tandem running" (ie: in single file), and the front individual escaped around 60% of the time, and the back individual on around 70% of trials (which is significantly better than alone). But both escaped only about 30% of the time. Being the back runner in a pair was the best position for escape, but the front individual was also better off than being alone (figure 1.2).

² That is 30% success rate for predator.



(Data from Li et al 2013 table 1 p200)

Figure 1.2 - Percentage of trials that an individual termite escaped the predator.

2. Many eyes effect ³.

Greater predator detection. Individual vigilance declines with increased group size, and this allows an individual to feed more without the loss of predator detection because of the "many eyes". This situation is beneficial for the individual if there is not a reduction in corporate vigilance (ie: nobody watches for predators), and there is a means of communicating the presence of a predator (ie: alarm signal given by the individual who detects predator). It also depends on whether the vigilance of another group member can be trusted or is valued as highly as own vigilance. Some animals have sentinel systems where an individual (or individuals) is clearly responsible for vigilance (appendix 1A).

But the ability of some individuals in the group to be vigilant may be limited because their vision is obscured by other group members. So, an individual can only enjoy the extra feeding time if they do not need to behaviourally monitor others all the time (ie: check that others are being vigilant as you feed) (Roberts 1996) ⁴.

3. Confusion effect.

Increased difficulty for predator to capture an

³ Also called the "collection detection effect" or "group vigilance hypothesis" (Roberts 1996).

⁴ On the other hand, the risk of individual predation may simply be less because of being part of a group (dilution effect), which is Roberts' (1996) argument.

individual ⁵. As predators have to process more information with multiple targets, the accuracy of processing declines, which produces the confusion effect. This effect may reduce the amount of attacks (as more processing resources are required which makes the predator vulnerable to its own predators), and the probability of success (ie: less kills per attack - low attack-to-kill ratio) (Ioannou et al 2008).

In three sets of laboratory experiments, Ioannou et al (2008) showed that the three-spined stickleback (*Gasterosteus aculeatus*) (figure 1.3) was less successful at capturing its prey (freshwater water flea; *Daphnia magna*; figure 1.4) as the group size increased. In the first experiment, the attack success (number of kills divided by number of attacks) during thirty minutes was significantly less ($p = 0.002$) ⁶ for a group of twenty prey (86%) than for a group of 500 (67%) for thirteen tested sticklebacks. The sticklebacks were tested in both conditions with one week apart, and in a random order.



(Source: Viridflavus)

Figure 1.3 - Three-spined stickleback.

Targeting errors (ie: the distance between the unsuccessful strike and the prey) significantly increased with group size. In the second experiment, the stickleback was shown prey (in 5 or 20 group sizes) in another compartment of the tank. Frame by frame analysis of video recording showed where the stickleback's snout touched the tank wall in comparison to the prey. Twenty trials were performed with each group size.

⁵ Predators counter this problem by targeting stray members of the group.

⁶ Using the Wilcoxon (T) matched pairs signed-ranks test which is the appropriate non-parametric statistical test of inference for repeated measures/related designs with data that does not fulfil the criteria for a parametric test. It compares the central tendency of two related samples.



(Source: Hajime Watanabe;
<http://www.plosgenetics.org/article/browseIssue.action?issue=info%3Adoi%2F10.1371%2Fissue.pgen.v07.i03>)

Figure 1.4 - Female adult *Daphnia magna*.

The final experiment compared group size in terms of number of prey and density or area of group. It was found that the greater number of prey produced a lower attack success not the density or area of the group.

1.2. ODDITY EFFECT

The benefits of the group for hiding within is reduced by the oddity effect (ie: more conspicuous individuals will stand out in the group and more likely attract the attention of predators). So, individual animals should seek groups of individuals who are similar in appearance to remove this risk (Rodgers 2011).

For example, the fish, sheepshead swordtails (*Xiphophorus birchmanni*) preferred a shoal of similar sized individuals over dis-similar body size when offered two groups of the same size (Wong and Rosenthal 2005), while another fish, sailfin mollies (*Poecilia latipinna*), have been found to prefer similar over dis-similar body colouration rather than body size (Bradner and McRobert 2001).

Rodgers et al (2011) investigated the choices made by Trinidadian guppies (*Poecilia reticulata*) (figure 1.5) between similar individuals ("matched shoal") and large dis-similar groups ("unmatched shoal")⁷.



(Source: H.Krisp)

Figure 1.5 - Female guppy.

One hundred and twenty female guppies (made up of 60 small and 60 large fish) were individually tested in the binary choice trials in the laboratory. Two plastic containers of fish were placed in the aquarium (one at each end) and the choice of the test fish was observed. There were six conditions based on the size of the unmatched shoal (figure 1.6).

⁷ Choice of the "matched shoal" reduces the oddity effect, while choice of the "unmatched shoal" increases the dilution effect.

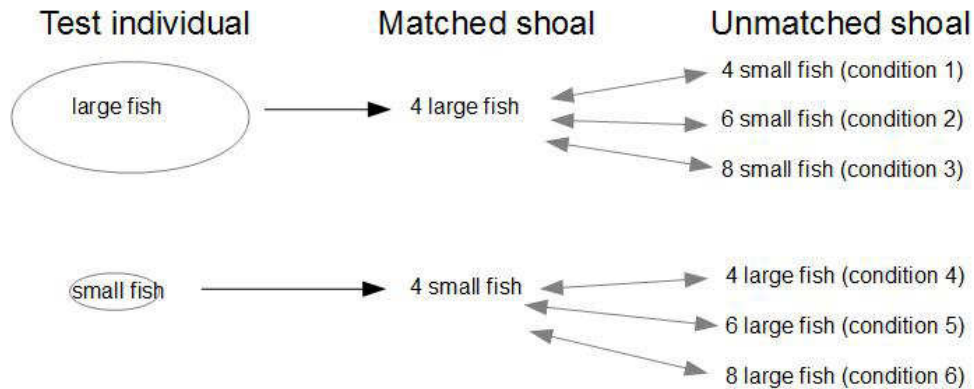


Figure 1.6 - Conditions in experiment by Rodgers et al (2011).

Large individuals (but not small fish) showed a significant preference for the matched shoal (irrelevant of the size of the unmatched shoal). This makes sense as larger fish are more attractive to predators (ie: greater calories), and also are more likely to be conspicuous in a group.

In observations of pools in seven rivers in Trinidad, Rodgers et al (2011) noted that as predator risk increased (as measured by number of predators nearby), all guppies preferred larger shoals (irrelevant of matched body size or not). The observations were made every ten seconds for a ten-minute period from the riverbank. Each of the seven rivers was ranked for abundance of predators.

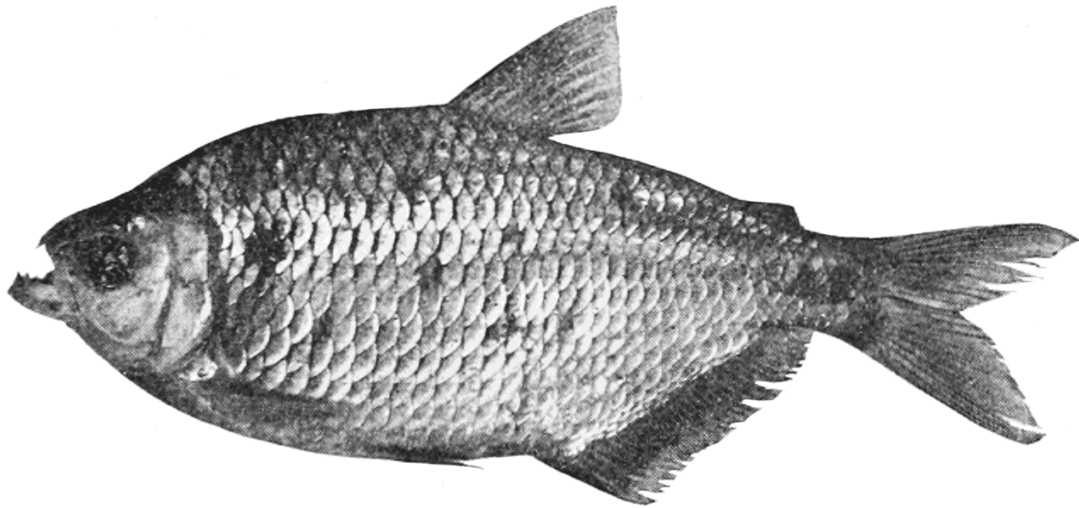
1.3. SELFISHNESS

The term used is the "selfish herd effect" (Hamilton 1971) - ie: "animals living in groups to reduce their individual predation risk by associating with conspecifics" (Goulart and Young 2013). Thus it encourages passive selfish behaviour. For example, the benefits are greatest for individuals at the centre of the group (ie: hidden behind outer members).

But taken to the extreme, it becomes the problem of "free-riders" - individuals who benefit from group living without paying the costs (eg: not watching for predators sometimes). Such individuals may also show active selfish behaviour (eg: injure or expose another individual to predators). In long-term groupings, individuals being actively selfish would be punished by the group, if not risk retaliation from the victim (unless the victim dies) (Goulart and Young 2013).

Goulart and Young (2013) investigated the active

selfish behaviour of deliberate injury to another group member to draw the predator away from the self in laboratory experiments with a school of fish in Brazil called two-spotted astyanax (*Astyanax bimaculatus*) (figure 1.7). Such aggressive behaviour triggers a chemical signal of injury that can be detected by the predator, and the injured individual is physically isolated.



(Source: Popular Science Monthly volume 68, 1905-6; in public domain)

Figure 1.7 - Two-spotted astyanax.

The fish were tested in groups of eight in four conditions:

i) Active search predator - A model of a predator fish, trahira (*Hoplias malabaricus*) chases the group. It was predicted that one group member attacking another group member would be an advantage for the attacker here because chasing predators look for vulnerable or weak animals in a group.

ii) Sit-and-wait predator - The same predator model but stationary. No need for a group member to be aggressive towards others as such predators go for the nearest prey.

iii) Aerial predator - A model of a bird pecking into the water. It was predicted that group members would not attack each other as birds cannot detect the chemical signals in the water of an injured fish.

iv) Control - A plastic bucket is placed into the water.

Only in the active search predator condition did the two-spotted astyanax show significantly more aggression towards group members.

So the risk of active selfish behaviour in a group is another disadvantage of flocking etc, along with competition for resources, and the risk of pathogen infection, for instance (Goulart and Young 2013).

1.4. APPENDIX 1A - SENTINEL BEHAVIOUR

Sentinel behaviour is different to group vigilance in that it is co-ordinated (with one group member clearly watching while the others forage), and the sentinel takes position (eg: elevated) that increases visibility (both in terms of seeing the predator but also exposing themselves to it) (Ridley et al 2013).

There are two main explanations for sentinel behaviour - co-operative or selfish behaviour. In the first case, a group member puts themselves out for the rest of the group either because they are kin or because of reciprocal altruism with non-kin (ie: "tit-for-tat").

On the other hand, Bednekoff (1997) proposed a selfish explanation for sentinel behaviour. Being a sentinel is the safest behaviour for an individual who has fed (ie: satiated) as they can detect a predator sooner than other group members and escape. So, it is predicted and empirically supported that individuals given food will become sentinels ⁸, and that they tend to be closer to the safety of cover, and suffer lower predation than foragers (Clutton-Brock et al 1999 ⁹). Ridley et al (2013) asked: "why do satiated individuals become sentinels instead of simply resting beneath or near cover, where they would be protected from predator attack?".

Ridley et al (2013) presented evidence for the co-operative explanation of sentinel behaviour from observations of the pied warbler (*Turdoides bicolor*) in the southern Kalahari Desert, South Africa. This bord

⁸ Clutton-Brock et al (1999) gave ten meerkats extra food at the beginning of one day (supplementary feeding), and these individuals increased their sentinel (guarding) time by about one-third compared to their average over the previous five days. In another experiment, meerkats were given extra food for thirty consecutive days, and they were sentinels three times as often as matched controls. Clutton-Brock et al (1999) concluded: "Our results provide no indication that the alternation of raised guarding depends on social processes more complex than the independent optimisation of activity by individuals, subject to nutritional status and the presence (or absence) of an existing guard. Though individuals rarely take two protracted turns at raised guarding in succession, there is apparently no regular rota..." (p1643).

⁹ Based on observations of six different groups of meerkats (*Suricata suricatta*) in Kalahari Gemsbok Park, South Africa.

lives in groups of up to ten adults, and is at risk from aerial predators (eg: raptors) and terrestrial ones (eg: mongoose). The distance to cover (eg: dead tree, shrub) of the sentinel was estimated relative to all group members.

It was found that sentinel behaviour was costly to the individual because:

a) Sentinels were targeted more often than foragers (eg: 13 of 16 raptor attacks).

b) Sentinels were further from cover than foragers (mean: 2.4 vs 1.6 m).

c) Sentinels took longer to reach cover after alarm calls than foragers (mean: 4.5 vs 1.9 secs).

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2. SOCIAL EAVESDROPPING

- 2.1. Chimpanzees
- 2.2. Domestic dogs
- 2.3. Appendix 2A - Social learning
- 2.4. Appendix 2B - Buttelmann and Tomasello (2013)
- 2.5. Appendix 2C - Kundera et al (2011)
- 2.6. References

2.1. CHIMPANZEES

Individual trial-and-error learning can be time-consuming and risky, so social learning is a valuable addition for animals (appendix 2A). This is learning from observing others. When it is observing another interaction, it is classed as "social eavesdropping"¹⁰. For example, chimpanzees preferred human A who had been seen to give food to human B rather than human C who was not generous (Subiaul et al 2008; table 2.1). The chimpanzees had eavesdropped the information that human A is generous without having to find this information by trial-and-error. This is known as "reputation attribution"^{11 12}.

- In the first experiment, seven chimpanzees at the New Iberia Primate Research Centre, Louisiana, USA, individually observed two unfamiliar humans with a familiar animal trainer. One of the unfamiliar humans always gave the trainer food in response to a gestural request (generous donor) and the other human consistently did not (selfish donor). Then the chimpanzees could approach either unfamiliar human and beg for food.

On average 57% of the chimpanzees chose the generous donor on the first trial, which is not statistically significantly above chance. In other words, they "did not spontaneously predict the future actions of humans, given the opportunity to indirectly observe exchanges" (Subiaul et al 2013).

Subiaul et al (2013) suggested a number of reasons for the findings including that the chimpanzees "may have great difficulty discriminating between two unfamiliar humans", and they "may have failed to make a connection between the behaviours of human donors directed towards another human and the future behaviours of those same humans directed towards them".

- In the second experiment, the chimpanzees observed the same

¹⁰ Parejo and Aviles (2007) defined eavesdropping as "the behaviour involving the extraction of information from signalling interactions between others" (quoted in Subiaul et al 2008).

¹¹ "Humans, unlike other primates, regularly interact with strangers... This feature of human sociality may have favoured the evolution of a cognitive system that assigns reputations to others. Reputation judgments involve the attribution of stable character traits or behavioural dispositions to specific individuals in a flexible and adaptive manner" (Subiaul et al 2008 p611)..

¹² Bshary and Grutter (2006) found that client fish preferred cleaner fish who had been observed to clean other clients rather than feed upon them. Cleaner fish are small fish that are allowed to enter the mouths of larger fish to eat parasites, but they can bite the client fish if they are selfish.

interaction as above until they had been trained to choose the generous donor every time. In fact, only four of the seven animals succeeded in being trained. Then these four chimpanzees were tested with a trial involving unfamiliar humans, and they chose the generous donor significantly more than chance. This was an example of transfer learning.

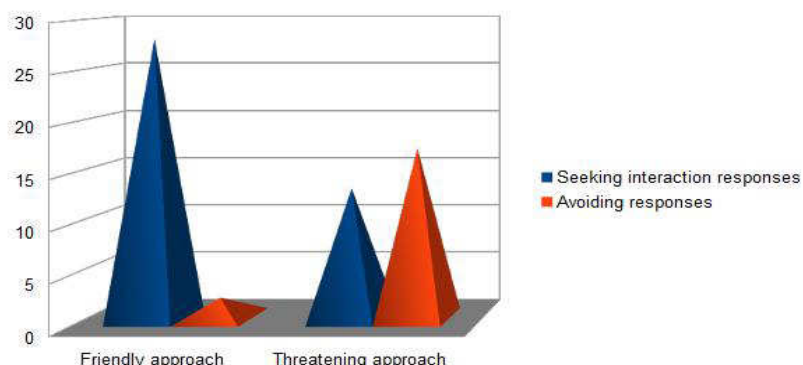
- In the third experiment, these four chimpanzees observed generous and selfish human donors acting towards another chimpanzee, and three of the observers showed a preference for the generous donor.
- Only a small number of chimpanzees took part in these experiments.

Table 2.1 - Details of Subiaul et al (2008).

2.2. DOMESTIC DOGS

Freidin et al (2013) were interested as to whether domestic dogs (*Canis familiaris*) could socially eavesdrop in this way. Studies have shown that dogs respond to human social cues, like discriminating between a friendly and a threatening stranger (Vas et al 2005; table 2.2), between expressions of happiness and disgust (Buttelmann and Tomasello 2013; appendix 2B), and between a sad and a neutral reaction (Custance and Mayer 2012; table 2.3).

- Thirty dog owners and their pets at a dog training school in Budapest, Hungary were involved. The dog seated with their owner was approached by a friendly stranger (speaking in a friendly manner and making eye contact) and a threatening stranger (staring at the dog without speaking). Significant different responses were observed (figure 2.1). "The majority of dogs showed cues of tolerant, friendly behaviours upon Friendly approach by the Stranger, many of them gave various signs of avoidance or aggressiveness when the Stranger approached them threateningly" (Vas et al 2005 p111).



(Data from Vas et al 2005 table 2 p107)

Figure - Number of dogs showed response to approach.

Table 2.2 - Vas et al (2005).

- Eighteen medium-sized dogs belonging to owners in the north-west USA were tested in their homes. Each dog experienced four conditions, which were counterbalanced, and lasted 20 seconds: their owner pretending to cry (eg: covering the face with hands), a stranger pretending to cry, their owner humming ("Mary Had a Little Lamb"), and a stranger humming. The dogs' responses in each condition were categorised as "person-oriented" (eg: approaching sniffing, licking, pawing human) or "non-person-oriented" (eg: sitting, lying down, walking around room).
- Significantly more dogs showed person-oriented behaviours during crying than humming. The style of approach was also more often submissive (than alert or playful).
- The authors noted with caution: "The dogs' pattern of response was behaviourally consistent with an expression of empathic concern, but is most parsimoniously interpreted as emotional contagion coupled with a previous learning history in which they have been rewarded for approaching distressed human companions" (p851).

Table 2.3 - Custance and Mayer (2012).

Kundey et al (2010) (appendix 2C) used the generous/selfish demonstrator paradigm to investigate social eavesdropping. Dogs observed a generous human who always gave food to a begging human, and a selfish demonstrator who did not. The dogs were then allowed to choose one of the two humans, and they usually preferred the generous human. But this study had no control group (Freidin et al 2013).

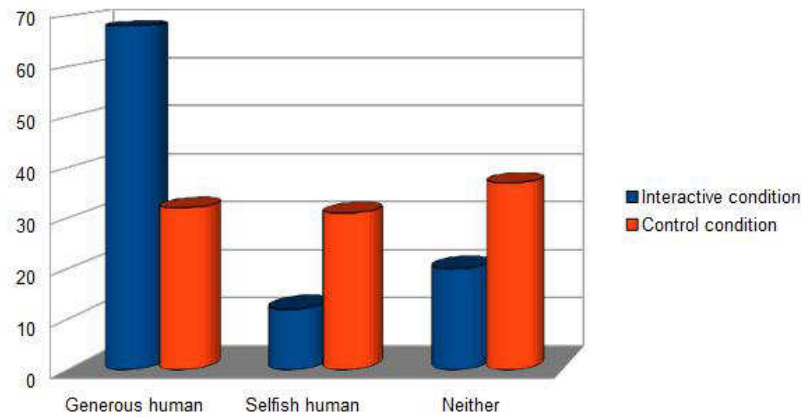
Marshall-Pescini et al (2011) replicated the experiment with a phantom control group using 100 dogs and their owners in Italy, who were recruited via personal contacts of the researchers, advertisements in parks, and veterinary surgeons. The demonstrators acted generous or selfish without the presence of a begging human¹³. The observing dogs did not show a preference for either human in the control condition, but only in the interactive condition¹⁴ (in the voice group) (figure 2.2).

Both these studies did not vary the reaction of the begging human to receiving the food. Freidin et al (2013) added this element to their experiments.

The researchers recruited 72 domestic dog-owners in Argentina. In the homes of the dogs, the experiment was set up. It involved two female donors and a begging male (figure 2.3). The donors stood at different ends of the room eating cornflakes. The beggar approached the

¹³ The humans still said the same words as in the interactive condition.

¹⁴ In front of a dog, two humans are eating food when approached by a third person (the beggar). One human says "no" to the request for food, and the other says "have it". This was the voice group. There was a gestures only group. The procedure was done six times before the dog is allowed to choose one of the eating humans.



(Data from Marshall-Pescini et al 2011 table 1 p1180)

Figure 2.2 - Mean percentage of dogs making first approach.

"positive" donor who gave him food, and the beggar responded with pleasure. The beggar approached the "negative" donor, but rejected the food he was given after tasting it. Versions of the scenario were run with gestures and verbal cues by the beggar (GV), gestures only (G), or verbal only (V). After observing six interactions, the dog was given ten seconds to choose between the donors.

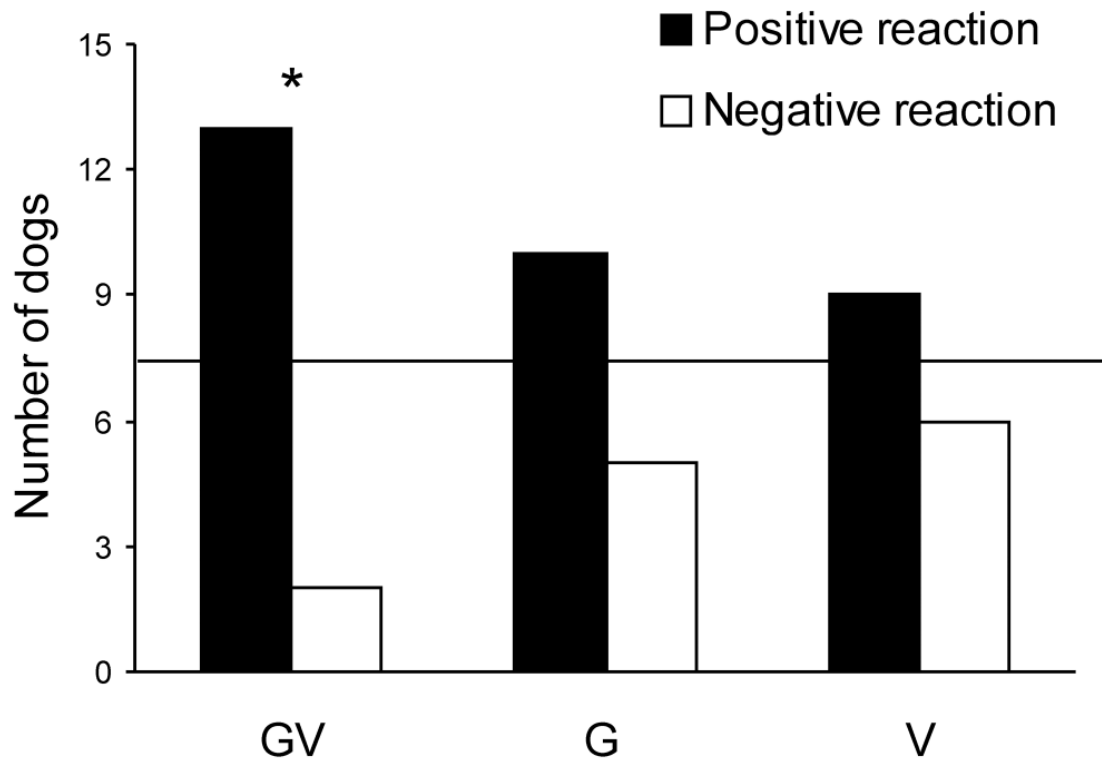


((A) The beggar receives food from the positive donor. (B) The beggar turns his back to the negative donor after having rejected the food. (C) The dog chooses the positive donor after the beggar left the room. All persons that appear in this figure have given written informed consent to publication of their photograph)

(Source: Freiden et al 2013 figure 1)

Figure 2.3 - Experimental set up and procedure.

The dogs chose the positive donor significantly more often than chance in the GV condition only (13 of 15 dogs that showed a preference) (figure 2.4).



(GV = beggar's reaction to the donors involved gestural and verbal cues, gestural cues alone (G), or verbal cues alone (V). The horizontal line in the middle of the figure denotes the 0.50 chance level. * = $P < 0.05$)

(Source: Freiden et al 2013 figure 2)

Figure 2.4 - Number of dogs choosing each donor.

Freiden et al (2013) felt that the results were promising: "The indirect attribution of reputation to donors based on the beggar's reaction in group GV implies a sequence of information processing stages. First, it implies the discrimination of the beggar's positive and negative reactions. This assumption is consistent with studies showing that dogs are capable of discriminating some human emotional expressions... Second, it may involve the association of the beggar's reaction with the corresponding donor, even when both donors displayed the same behaviours. Last, it requires remembering the learned association at the moment of choice (when the beggar was not present anymore), which would lead them to prefer and approach the positive over the negative donor" (p4). However, other interpretations and variables may be involved.

Thus, Freiden et al (2013) ran two other versions of the experiment to check for other variables that could explain the preference for the generous donor (known as local enhancements).

Firstly, the dogs may have associated the positive and negative reactions of the beggar with the places

where the donors stood rather than the donors themselves. In the second experiment with 23 more dogs ¹⁵, only the GV condition was used, but the donors changed positions in the room three times between the six interactions. The same person was the positive donor and the same was the negative throughout the interactions. Five dogs made no choice, nine preferred the positive donor, and nine the negative one when given the choice. This was not significantly different to chance. The researchers admitted that the "negative result might be the consequence of confusion by the dogs (because the donors switched places many times) and insufficient experience with the situation" (Freiden et al 2013 p4).

In the third experiment ¹⁶, a non-social version with 27 more dogs was tried. This involved two platforms containing plates of food, and the beggar approached each in turn, tried the food, and reacted positively to one and negatively to the other as in the GV condition before. The dogs showed no significant preference for either platform (figure 2.5), which "helps discard the possibility that dogs made an inference about the quality of the food in each side based on the beggar's reaction" (Freiden et al 2013).

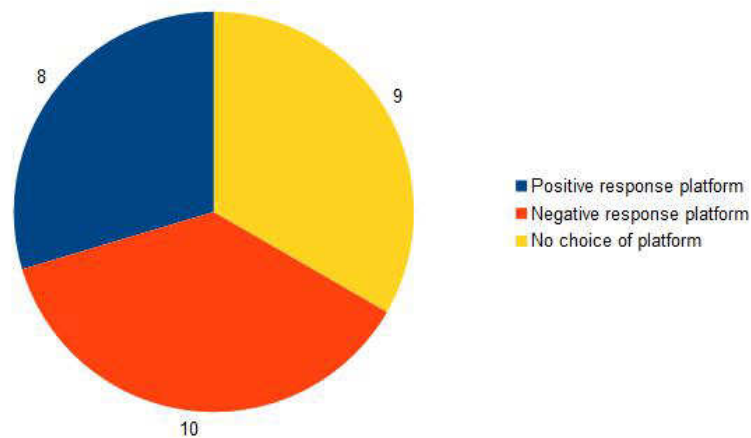


Figure 2.5 - Number of dogs choosing each platform.

Overall, Freiden et al (2013) felt that their experiments showed that the observing dogs did respond to the beggar's behaviour, but where the donor was standing was also important (ie: local enhancement). "Nonetheless, we did not find conclusive evidence that dogs discriminate the donors by their physical features, which is a prerequisite of reputation attribution" (Freiden et

¹⁵ Actually called experiment 1b by researchers.

¹⁶ Experiment 1c.

al 2013 p1).

Nitzschner et al (2012) tried a variation of social eavesdropping by allowing 32 dogs to individually observe a "nice" human and a "ignoring" human interactive with a dog. The former stroked the dog while the "ignoring" human did nothing with the dog (figure 2.6)¹⁷. The observing dogs showed no preference for either human when given the choice (figure 2.7). Freiden et al (2013) wondered whether "the use of social reinforcement, instead of food, might make it harder for dogs to form a preference for people they observe interacting with third parties"¹⁸.

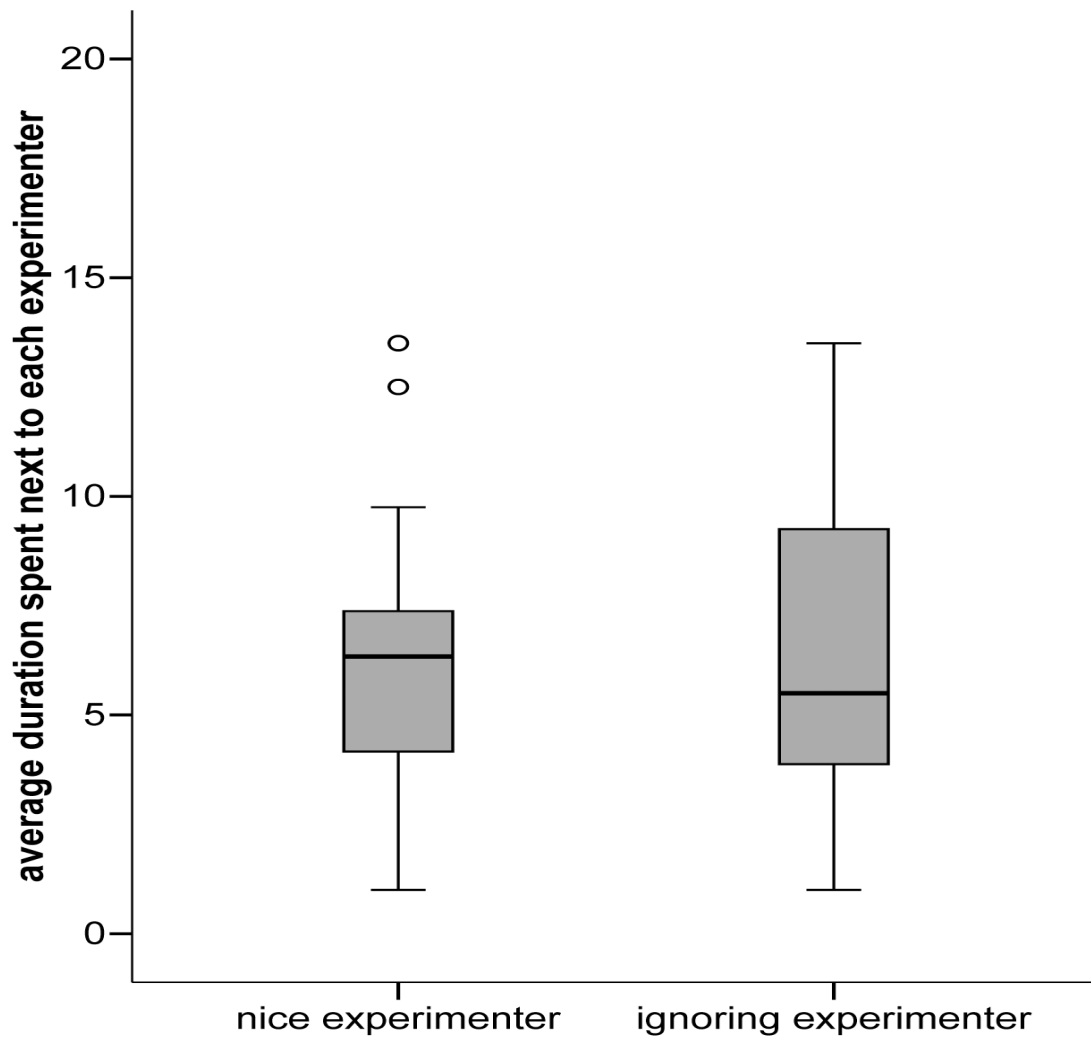


(Source: Nitzschner et al 2012 figure 3)

Figure 2.6 - Photographs of experiment design with nice experimenter (A) and ignoring experimenter (B).

¹⁷ Nitzschner et al (2012) admitted that the "ignoring" human may have been perceived as "a human who went for a walk with the demonstrator dog".

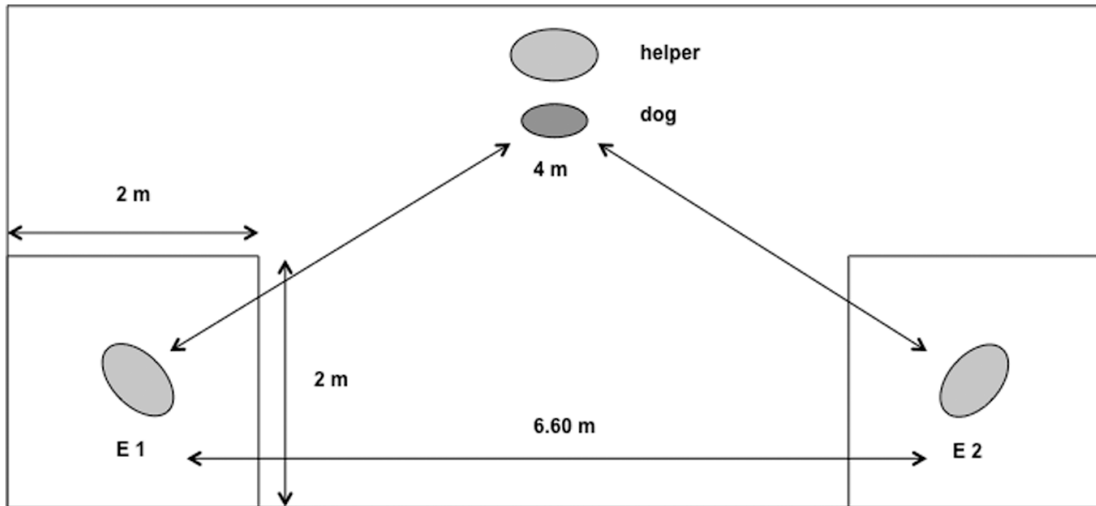
¹⁸ Nitzschner et al (2012) explained why they did not include a food reward: "We are aware of the high motivating effect of food, but we encountered several problems with the use of food in this kind of setup in an extensive pilot study... In this pilot phase, we found that the dogs did not develop a preference for the 'giving donor', even after many direct experiences. A possible explanation for this could be that the dogs focused their attention on the food more than on the behaviour of the experimenters".



(Source: Nitzschner et al 2012 figure 4)

Figure 2.7 - Median (and inter-quartile) time spent near nice or ignoring human after observing interactions with other dog.

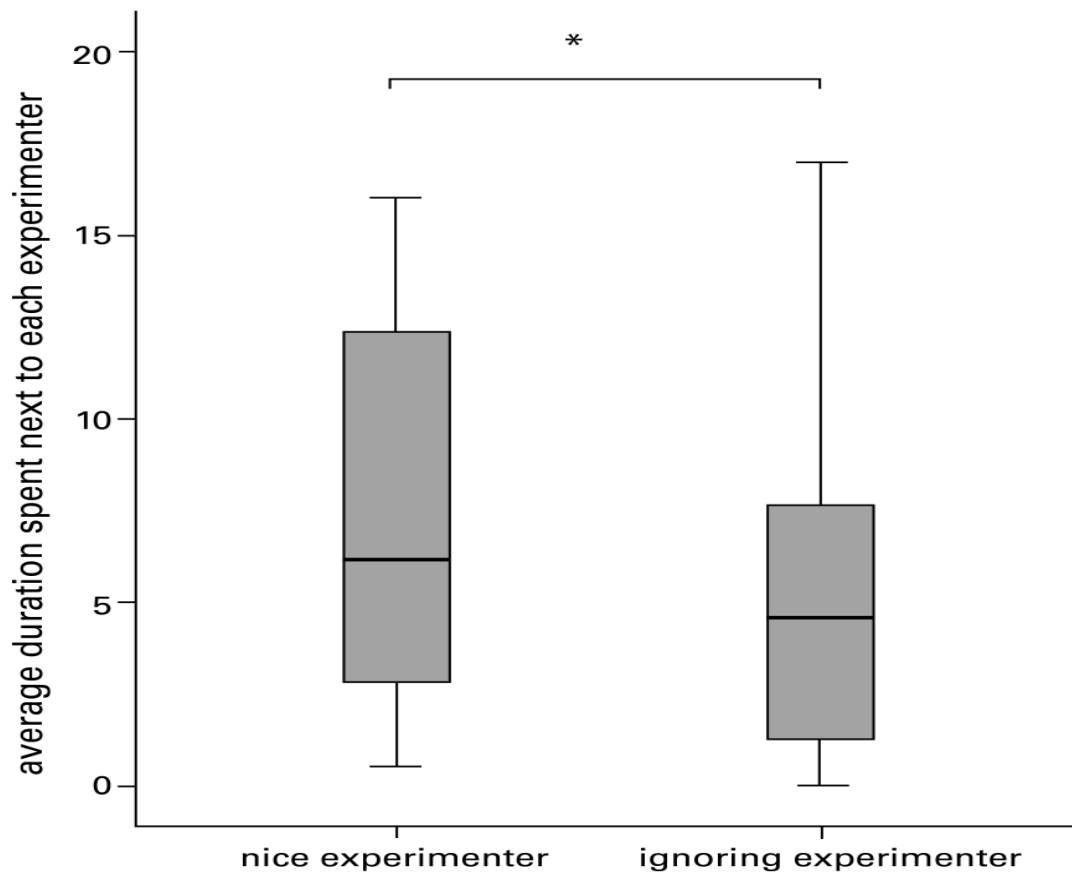
However, the dogs preferred the "nice" human when the previous interaction had been with themselves. In the first experiment, 32 more dogs belonging to owners in Germany interacted with the "nice" human (who petted the dog, and talked to it) or the "ignoring" one (who walked pass the dog without talking to it or making eye contact). When given the choice of human (figure 2.8), nineteen dogs preferred the "nice" and thirteen the "ignoring" one (which was not significant), but the dogs did spend significantly more time around the "nice" human (figure 2.9).



(E = experimenter - ie: human who was nice or ignoring; the position was counterbalanced. Entry into 2m area around human was counted as approaching and timed)

(Source: Nitzschner et al 2012 figure 1)

Figure 2.8 - Set up of experimental choice.



(Source: Nitzschner et al 2012 figure 2)

Figure 2.9 - Median (and inter-quartile) time spent near nice or ignoring human after interaction.

2.3. APPENDIX 2A - SOCIAL LEARNING

Thonhauser et al (2013) outlined different types of social learning (defined as a naive animal acquiring information from a knowledgeable one):

i) Drawing the observer's attention to a particular object (stimulus enhancement) or location (local enhancement).

ii) Observing the reward attached to a particular stimulus (observational conditioning).

iii) The presence of a demonstrator encourages the observer to engage in similar behaviour (social facilitation).

iv) The observer copies the action of the demonstrator in the same situation (contextual imitation) or generally (production imitation).

Thonhauser et al (2013) showed an experimental example of contextual imitation with freshwater stingrays (*Potamotrygon falkneri*) from Peru. Naive individuals were presented with a plastic tube containing food.

The number of trials it took individuals to extract the food ¹⁹ (control) was significantly more than for animals who had observed a demonstrator for five trials beforehand (mean: 45 vs 17) ²⁰.

Observers also showed a greater frequency of the most efficient strategy to extract the food ("suck and undulation" ²¹).

2.4. APPENDIX 2B - BUTTELMANN AND TOMASELLO (2013)

Buttelmann and Tomasello (2013) felt that "some domestic dogs recognise both the directedness and the valence of some human emotional expressions" (p137).

They tested 58 dogs from five breeds using a paradigm of Repacholi (1998) with 14 month-old human infants. An adult approaches two open boxes in turn (where the contents are hidden from the observer) and produces a different facial expression for each one (eg: happy or disgust). The child is then offered a choice of

¹⁹ Success was defined as extracting the food in ten consecutive trials.

²⁰ There was a thirty-minute gap between observing and the opportunity to imitate. this interval allowed the researchers to say: "we suggest that the observer's response might be imitation, and not simply a reflexive response or a less complex form of social interaction such as local enhancement, social facilitation, or observational conditioning..." (Thonhauser et al 2013 p931).

²¹ This involved fin movements to produce a water current to move the tube towards the individual (undulation), and placing mouth on tube and sucking out food.

the boxes.

Buttelmann and Tomasello (2013) had two experimental conditions: Happy-Neutral and Happy-Disgust. There was also a control condition where two boxes were presented without a human looking into them.

The dogs chose the "happy" box in 52.1% of the trials of Happy-Neutral, and 54.9% in the Happy-Disgust condition. The latter figure was statistically significant compared to chance. Buttelmann and Tomasello (2013) noted that "although dogs as a group chose the box with the positively evaluated content in the Happy-Disgust condition their individual levels of preference were relatively low. This makes us cautious regarding the robustness of dogs' knowledge about human emotional expressions as indicators for the location of food" (p143).

2.5. APPENDIX 2C - KUNDEY ET AL (2011)

Kundey et al (2011) explored the dog's ability to socially eavesdrop in six experiments.

Experiment 1 (basic design) - Ten dogs observed one human consistently give food to a begging human and one human withhold food in ten face-to-face exchanges. All dogs chose the giving demonstrator.

Experiment 2 - The humans interacted as above but the two demonstrators were facing away from the beggar. The researchers "reasoned if face-to-face contact between parties in an observed exchange is necessary for dogs' reputation-like inference, then dogs should choose demonstrators at chance when face-to-face contact is removed. Alternatively, if face-to-face contact between parties in observed exchanges is not necessary for dogs' reputation-like inference, dogs should show a preference for the giving demonstrator" (p294). Eight of nine dogs chose the giving demonstrator, which supported the latter hypothesis.

Experiment 3 - In this experiment the demonstrators were hidden in large boxes. The researchers hypothesised: "If the visual social cues emitted by the demonstrators are important to dogs' reputation-like inferences, dogs should choose the 'withholding' and 'giving' boxes at chance when we reduce the demonstrators' ability to signal such cues. Alternatively, if social cues emitted by the demonstrators are not necessary for dogs' indirect reputation-like inferences, dogs should show a preference for the 'giving' box" (p295). Nine of the ten dogs preferred the "giving" box.

Experiment 4 - This experiment removed the two demonstrators, and the begging human interacted with two small moving boxes (one providing treats, the other not). "If, ... a living, animate agent is not necessary as a recipient of the demonstrators' actions, dogs should show a preference for the giving demonstrator even when we replace the human recipient with a non-human, inanimate self-propelled box" (Kundey et al 2011 p296). All ten dogs chose the giving moving box.

Experiment 5 - The begging human was removed in this experiment, and the two demonstrators either placed food in a small box or not. The average choice of the giving demonstrator was 2.75 out of six trials for each of twelve dogs. Kundey et al (2011) pointed out: "Thus, dogs did not choose the giving demonstrator significantly more often than the withholding demonstrator when the 'giving' and 'withholding' appeared inadvertent" (p298).

Experiment 6 - This experiment was designed to control any local enhancements that could have accounted for the previous findings. This involved the demonstrators changing places after giving or withholding food and before the dog made their choice²². All ten 10 dogs chose the giving demonstrator.

Another variation included was the position of the beggar. In all the previous experiments, the participants were seated (or kneeling) on the floor. In this case, the demonstrators were seated on chairs and the beggar stood close to them. Nine of ten dogs approached the giving demonstrator first.

These two variations showed that the dogs were not just making choices "based on a particular location associated with reward" (Kundey et al 2011).

Altogether, the findings "suggest dogs can derive and act on information about unfamiliar individuals through reputation-like inferences by observing third-party interactions - an ability previously thought to be exclusive to the hominid clade and possibly members of the primate order..." (p300).

Subiaul et al (2008) distinguished an abstract ability of reputation inference, which is used flexibly in new situations (by humans), and "domain-specific skills that function analogously to reputation judgments"

²² The beggar also faced the wall at this point, in order to control for the "Clever Hans" effect. "Clever Hans" was the name given to a horse in Germany who appeared to be able to count. The owner would say a simple sum (eg: 2 + 3), and the horse would stamp its foot the correct number of times. In fact, the animal was sensitive to unconscious social cues by the owner (eg: smiling when the correct number of stamps produced) (Pfungst 1907/1911).

(p612) (eg: awareness of dominant animal in social hierarchy). Kundery et al (2011) could not say which of these skills the dogs in their experiments showed, but "the significant number of dogs choosing the 'giving' demonstrator, absent differential reinforcement, across a variety of unfamiliar contexts suggests some flexibility" (p300).

Table 2.4 summarises the different designs of the six experiment by Kundery et al (2011).

Expt	Design	Dogs choosing giving demonstrator
1	Basic design: Face-to-face interaction between two demonstrators and beggar.	10/10
2	Demonstrators face away from beggar.	8/9
3	Demonstrators hidden in large boxes.	9/10
4	Demonstrators replaced by two small moving boxes.	10/10
5	No beggar. Demonstrators placed food in tray or not.	median 2.75 of 6 trials for 12 dogs
6	Demonstrators moved position before dogs chose. Demonstrators on chairs and beggar standing.	10/10 9/10

Table 2.4 - Experiments by Kundery et al (2011).

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3. HONEST SIGNALS

- 3.1. Honest communication
- 3.2. Dishonest signalling
- 3.3. Stotting
- 3.4. References

3.1. HONEST COMMUNICATION

Zollman et al (2013) began: "Communication is ubiquitous in the biological world. When the interests of signaller and signal receiver are perfectly aligned, the evolutionary benefits of reliable communication are straightforward. But when interests are not aligned, signallers might be selected to manipulate signal receivers with misleading signals, and the signal receivers might evolve to disregard such communications". Situations of conflict of interests most often relate to mating and predator-prey interactions.

"Honest" communication means that the signal carries reliable information. For example, an animal produces signals of strength to an opponent which can be backed up by actual strength. But if the honesty of the signal is never tested, then cheaters will benefit. That is, individuals who can signal strength when they are weak (bluffing - "dishonest" communication)²³. On the other hand, if the signal is tested every time, then there is no benefit to signalling strength, say, to avoid physical confrontation²⁴.

Zahavi (1975) proposed the "handicap principle" by which only strong animals, for example, can give signals of this because of the cost (handicap) of showing their strength²⁵²⁶. The most quoted example is the male peacock's tail. Only genuine good quality individuals can maintain such a handicap that the size of the tail is an honest signal of quality²⁷. Signals that cannot be faked are classed as "indices". For example, the pitch of a toad's call is determined by body size (Higham 2014).

²³ It should be costlier for low-quality individuals to give high-quality signals than for high-quality individuals, or else cheaters will dominate (Grafen 1990).

²⁴ That is, the signal's "reliability being enforced by the social consequences of sending the signal associated with the more desirable state. In other words, weak individuals will avoid signalling that they are strong, even though this would allow them to defeat other weak individuals without contest, because by doing so they give up the chance to escape from confrontation with strong individuals" (Helgesen et al 2013 p1215)..

²⁵ Also called the "costly signalling theory" (Hawkes and Bliege Bird 2002).

²⁶ Grose (2011), for example, has challenged the handicap principle.

²⁷ "Handicaps" are "strategic" costs (costs related to maintenance of signal honesty) as opposed to "efficacy" costs (costs related to ensuring messages received) (Higham 2014).

3.2. DISHONEST SIGNALLING

There must be a cost to giving an inaccurate or dishonest signal that makes it not worth doing. For example, a rhesus monkey who gives a deceptive food call is physically attacked as punishment by other rhesus monkeys (Hauser 1992) ("punishment of cheaters" principle).

Male spotted bowerbirds (*Chlamydera maculata*) signal their quality through their nest (bower), particularly the number of *Solanum* berries on it. Males who are given extra berries by the researcher were punished by other male bowerbirds destroying the nest (Madden 2002). Madden (2002) added thirty berries to certain bowers in Taunton National Park, Queensland, Australia, and these experienced significantly more destructions than in normal years. Males also tried to remove the extras to return to their usual level.

In another experiment, all the berries were removed from the bower and left in a pile with extra berries nearby. Males only add the number that they usually had, despite the lack of energy cost to them of adding extra. "These results indicate that there may be a trade-off for a male between maintaining a high number of berries, and appearing attractive to females, and the increased risk of destruction of the bower associated with displaying high numbers of berries...It appears that certain traits may be highly beneficial to a male in terms of his mating success, but only if he is able to meet the cost of bearing them. If he cannot meet the cost, such a trait becomes instead, a hindrance" (Madden 2002 p1350)²⁸.

Alternatively, if the benefits of cheating are low, then individuals will not send deceptive signals.

Mimicry is a case of a dishonest signal. For example, an edible prey copying the appearance of a toxic prey. The mimic octopus (*Thaumoctopus mimicus*) can do impressions of toxic prey like the lion fish or the banded sea snake, for instance (Forbes 2011).

Crab spiders sit on flowers and wait to catch flying insects that come to the flower. Australian crab spiders have been found to reflect large amount of UV

²⁸ Madden (2002) concluded that "males capable of holding a large number of berries, without incurring elevated harassment by neighbouring males may offer a signal to visiting females of their social dominance or physical prowess. As such, berries may act as an 'honest' indicator to females of male quality, constantly patrolled by other males to ensure against cheats. The unusually large brains of the spotted bowerbird... may facilitate accurate comparisons of bower components between bowers in relation to others within the population. Therefore, the number of *Solanum* berries displayed can be viewed as a condition-dependent trait, in which trait expression is constrained by a male's relative quality within a population, and is closely monitored by peers" (p1350).

(ultraviolet) light, which acts as a deceptive signal that lures insects to the flower (ie: flower appears more inviting to insect) (Heberstein et al 2014).

Zollman et al (2013) proposed a compromise to honest and dishonest signals - ie: partially honest. High quality individuals will always be honest, whereas low quality individuals will sometimes send dishonest signals. Receivers will sometimes test the truth of these signals but never the absence of a signal.

For example, in relation to predator-prey interactions, a prey animal signals that it is too fast to be caught by the predator by not moving away immediately, say. Fast individuals (ie: high quality) will always produce this honest signal. Slow individuals (ie: low quality) are the cheaters when they use this signal, but it is a potentially costly strategy to use every time if the receiver (predator) randomly tests the signal by chasing sometimes. Thus the cheater uses the signal dishonestly only sometimes (ie: gambles that is not one of the times that the receiver ignores the signal) (table 3.1).

	Slow prey never uses dishonest signals	Slow prey uses dishonest signals
Predator chases every time	Signal no evolutionary benefit as ignored	Signal no evolutionary benefit as ignored
Predator always responds to signal	Chases easy-to-catch prey	Benefits to cheating and all prey evolve strategy
Predator sometimes ignores signal and chases prey	Catch prey sometimes	Makes cheating risky strategy (ie: gamble)

Table 3.1 - Options in predator-prey interactions and dishonest signals.

3.3. STOTTING

Stotting is "leaping off the ground with all four legs held stiff and straight" (Fitzgibbon and Fanshawe 1988). It is performed by adult Thomson's gazelles (Gazelle thomsoni) (figure 3.1) in response to a predator before and as the gazelle flees. Thomson's gazelles face two main strategies of predators - stalking and short chase (eg: cheetahs), coursing (ie: visible approach) and long-distance chase (eg: African wild dogs). Stotting in the former case signals that the stalker has been spotted, but, more importantly, with coursing predators, it is an honest signal of stamina and/or running speed

(Fitzgibbon and Fanshawe 1988) ²⁹.



(Source: Energo)

Figure 3.1 - Male Thomson's gazelle.

Fitzgibbon and Fanshawe (1988) collected over 2500 hours of daytime binocular-based observations of Thomson's gazelles in the Serengeti National Park, Tanzania (figure 3.2), between March 1985 and April 1987. This included 125 chases by African wild dogs, and 133 by cheetahs. The rate of stotting (ie: stots per second) and its duration were recorded.

The gazelles were significantly more likely to stot to hunting wild dogs than to cheetahs (78% of occasions vs 9%).

When faced with a group of gazelles, wild dogs

²⁹ This is called the "prey is healthy hypothesis" (Caro 1986a) (ie: "by stotting gazelles inform predators that they are healthy enough to outrun them"; Fitzgibbon and Fanshawe 1988), and it is one of eleven hypotheses proposed for the behaviour (Caro 1986a; 1986b).



(Source: Bamse)

Figure 3.2 - Location of national parks in Tanzania including the Serengeti in the north of the country.

selected the individuals who stotted significantly less (1.64 stots per second for chased individuals vs 1.86 for non-chased ones). Individual gazelles who escaped a chase were significantly more likely to stot (89%) than those captured (74%), and these individuals also stotted for longer durations during the chase.

Stotting was less overall during the dry season, when food is scarce and the gazelles are less able to escape, than in the wet season (when food plentiful) (1.4 stots per second vs 1.7).

Fitzgibbon and Fanshawe (1988) summed up: "we suggest that gazelles stot in order to advertise their ability to outrun predators and assume that physical condition is one important influencing factor. Any

gazelle stotting at a higher rate than those nearby signals that it will be more difficult to catch. Variation in the rate of stotting could allow predators to assess the ability of potential prey to escape" (p73).

But there is always the risk of cheaters. "Gazelles which are actually incapable of out-running the predators, might try and deceive them by stotting at high rates, but should be unable to perform deceitfully for long. Dogs could check for such cheating by continuing to chase suspicious gazelles for a critical period. In addition, the duration of continuous stotting that a gazelle could maintain or the average height of its stots could be additional indicators of its ability to outrun predators, more difficult to bluff than the rate of stotting" (Fitzgibbon and Fanshawe 1988 p73).

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4. COMPARATIVE COGNITION: MEMORY ABILITY OF HUMMINGBIRDS

- 4.1. Introduction
- 4.2. Experiments
- 4.3. References

4.1. INTRODUCTION

Healy and Hurly (2013) have studied the cognitive abilities of rufous hummingbirds (*Selasphorus rufus*) (figure 4.1) in the eastern Rocky Mountains (south-west of Beaver Mines), Alberta, Canada, for nearly twenty years³⁰. The memory for flowers previously visited was the focus of the research. The birds feed every 10-15 minutes because of their high energy expenditure, so data can be collected quickly.



(Source: US Fish and Wildlife Service; in public domain)

Figure 4.1 - Male rufous hummingbird.

³⁰ The researchers were performing field experiments (ie: researchers take the experiment to the environment of the participant). The experimental apparatus (artificial flowers) was used in areas of hummingbirds' territory.

In laboratory experiments, the memory of animals like rats is tested with the radial-arm maze, which involves a number of arms (eg: four) spreading out from the centre. Some contain food, and the task is to remember which arms do. This apparatus was adapted to the open-field feeding task for birds (Spetch and Edwards 1986).

A hummingbird will defend a territory of about two hundred flowers. Efficient foraging involves visiting sources of nectar and remembering those temporarily depleted (which require about four hours to replenish) (Healy and Hurly 1995).

Certain strategies can be used (Healy and Hurly 1995):

a) Visiting the flowers in a certain order ("trap-lining"; Feinsinger 1978) - this requires a memory for the pattern only.

b) Visiting clumps of flowers - this requires a memory for which clumps visited recently.

c) Visiting individual flowers and remembering which are depleted. Healy and Hurly's studies support this strategy.

4.2. EXPERIMENTS

The first set of experiments (Healy and Hurly 1995) showed the high level of memory abilities of the bird (which weighs 3 grams). Eight artificial flowers³¹ were placed in a circle³² with a different coloured disc attached to each. The birds (three males and three females) were allowed to feed from four "flowers", and then taken away³³. When they returned, would they remember which "flowers" were empty? Varying the interval from a few seconds (four seconds) to over an hour (77 minutes), the birds were more likely to visit "flowers" that were not emptied on the first visit (ie: significantly more often than chance)³⁴. This showed that the birds could remember where the flowers were located and which were empty³⁵.

It was the location that the birds seemed to remember. Hurly and Healy (1996) offered nine birds four different coloured artificial flowers, of which one (say, red) was filled with sugar solution (but too much to eat

³¹ A small well containing sugar solution on a 60 cm high wooden stake.

³² The circle is about 180 cm in diameter with 70 cm between the "flowers".

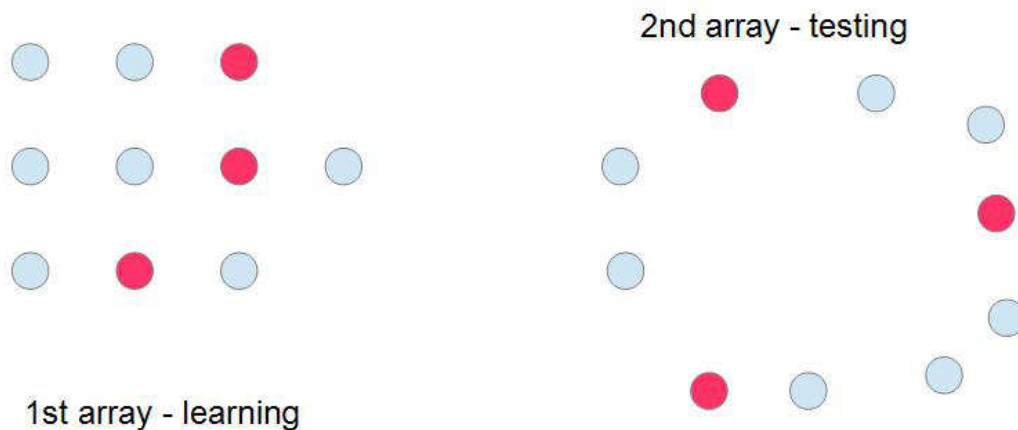
³³ In the "free" trial, all eight flowers contained food and after feeding on four of them, the bird is chased away by the experimenter. Then when it returns, will it remember which flowers had not been visited? In the "forced" trial, four flowers had food and the bird emptied them. They were refilled after the bird left to see if the bird would return to the same four later.

³⁴ Mean of about 70% (compared to chance of 50%) ($p < 0.05$). Five of the six birds were significantly above chance.

³⁵ Not all variables were controlled - eg: birds determined retention interval based on when they returned. "But in spite of not being able to control the birds' behaviour as thoroughly as one could in a laboratory situation, we were still able to assess memory performance" (Healy and Hurly 1995 p67).

in one sitting). The birds fed and left, and then the experimenters moved the location of the red "flower". The returning birds tended to go to the original location of this "flower" not pay attention to its colour.

However, Hurly and Healy (2002) showed that in different circumstances, the birds did remember colours. In this case, ten artificial flowers were offered, but only three contained food. For example, yellow "flowers" had food and red did not. After the birds had learned the colour-reward association, the flowers were moved two metres away to remove landmark cues. The experimenters discovered that they had to also alter the array of the flowers (eg: from a circle to a square) before the birds used the colour cues only to recall which "flowers" had food (figure 4.2).



(Red "flowers" contain food but blue do not)

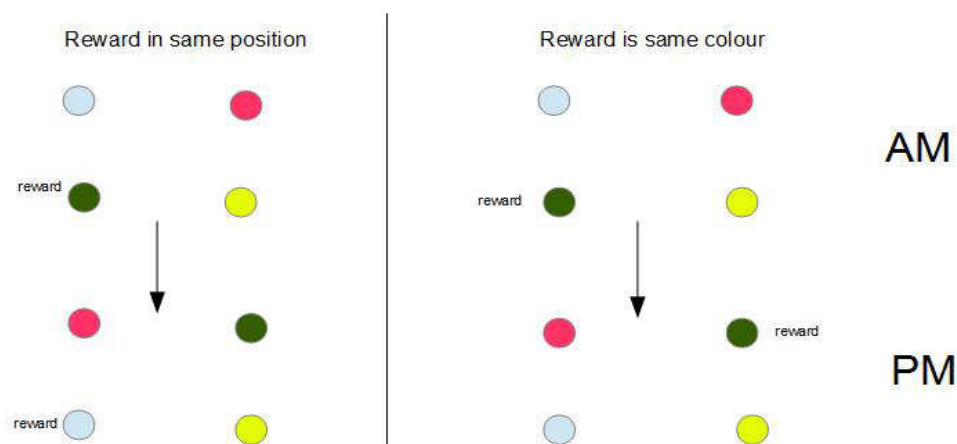
(Based on Healy and Hurly 2013 figure 6 p19)

Figure 4.2 - Example of how researchers might have changed array of artificial flowers in Hurly and Healy (2002).

Spatial memory relates to three-dimensions in the natural environment. Flores Abreu et al (2013) found that hummingbirds learned which "flowers" contained food faster when the "flowers" were presented along a horizontal pole (ie: at the same height) than on a vertical pole (ie: at different heights).

In other experiments, researchers found that the hummingbirds could recall time intervals. Henderson et al (2006) refilled four of eight artificial flowers that had been emptied every ten minutes, and four after twenty minutes. The three birds learned within one day to return to the ten minute-refilling "flowers" around every ten minutes and the twenty minute-refillers at around twenty minutes.

These experiments showed the three components of episodic memory: what-where-when (Healy and Hurly 2013) (table 4.1). One set of experiments attempted to test all these components together (Marshall 2012 quoted in Healy and Hurly 2013). Eight "flowers" of four different colours were presented, of which only one colour contained food. The colour of the reward "flowers" and the array were varied between morning and afternoon, but the position or the colour of the reward "flowers" remained the same in the two different arrays (figure 4.3). The birds did learn to find the "flowers" containing food (what) at the correct location (where) at the correct time of the day (when). Mistakes involved going to the location or colour for the different time of the day - thus "it is the when component that is the most difficult for the animal to get right" (Healy and Hurly 2013).



(Based on Healy and Hurly 2013 figure 8 p23)

Figure 4.3 - Example of how researchers might have changed array of artificial flowers in Marshall (2012 quoted in Healy and Hurly 2013).

Type of memory	How manifest
Spatial	Return to location of full flowers in relation to empty flowers after delay
Episodic - what	Remember which artificial flowers contain food
Episodic - where *	Remember location of food
Episodic - when	Remember when "flowers" have food

(* Spatial memory and where episodic memory are similar abilities)

Table 4.1 - Memory abilities of rufous hummingbirds.

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5. ANIMALS HAVING PERSONALITIES AND THE FEAR OF ANTHROPOMORPHISM

- 5.1. Introduction
- 5.2. Mammals
- 5.3. Primates
- 5.4. Birds
- 5.5. Appendix 5A - Boldness

5.1. INTRODUCTION

Individual patterns of behaviour that are stable across time and/or place are called "temperaments", "personalities", or "behavioural syndromes" (Zipser et al 2013) ³⁶. As soon as the idea of an individual animal having a personality is mentioned, there are concerns about anthropomorphism ³⁷ ³⁸. Furthermore, Zipser et al (2013) stated, "due to the novelty of the field, there are still conceptual and methodological difficulties..., and thus, the specific way this concept is applied and interpreted varies greatly in the field. For example, the use of the two logical operators and/or shows that it is by no means clear whether both temporal and contextual stability of behaviour are necessary to constitute animal personality" (p970) ³⁹.

In terms of these two aspects, there are certain issues to consider:

a) Time/temporal stability - eg: what is the time period for behaviour to be seen as a stable personality trait?

"In fact, many authors argue that personalities should be more flexible over long timescales than currently assumed. This makes sense from a life-history point of view because environmental conditions and thus selection regimes on associations of behaviours might

³⁶ Gosling (1998) noted that "the distinction between personality and temperament is often blurred. Moreover, some of the studies... refer to little more than individual differences in specific behaviours during a single testing situation" (p107). For example, "temperament" is sometimes used in non-social situations (eg: behaviour in a novel environment) and "personality" in social situations (eg: behaviour in group) (Freeman and Gosling 2010).

³⁷ This is the tendency to attribute human-like characteristics, behaviours, or emotions to non-human animals.

³⁸ Jane Goodall, who observed wild chimpanzees in African over many years, was one of the first people to use the idea of personality for individual animals. She was criticised for being anthropomorphic. "However, no empirical studies support claims that anthropomorphism is always inconsistent with valid scientific inquiry. Moreover, when anthropomorphism is used to generate testable hypotheses, an approach referred to as 'critical anthropomorphism', it can lead to a better understanding of complex animal behaviour" (Weiss et al 2012 p1355).

³⁹ "Apparently, it has become more scientifically acceptable, maybe even respectable, to study personality, temperament, and emotion in animals" (Gosling 1998 p113).

change throughout the lifespan of an individual" (Zipser et al 2013 p971) ⁴⁰.

b) Situation/contextual stability - eg: in how many different contexts must the behaviour be shown?

One technique has been to place animals in unfamiliar environments, and assess their willingness to explore it (boldness; appendix 5A), and then whether the animals show the same behaviour in response to predators, say (eg: Huntingford 1976 - bold and active sticklebacks take greater risks around dummy predators). On the other hand, a wider selection may be required (Zipser et al 2013).

Gosling (1998) noted five methodological issues for research into animal personality:

i) Ensuring that all potential traits are included.

ii) Problems in comparing the same trait across species. "Moreover, before applying the same trait to different species, researchers must consider the different ways in which that trait will be manifested by species with different behavioural repertoires living in different physical and social environments. For example, one would expect nervousness to be manifested differently in chimpanzees and in octopuses" (Gosling 1998 p114).

iii) Most studies involve captive populations, and the question is whether the findings are generalisable to the wild.

iv) Captive populations also tend to be small.

v) Dealing with subjectivity/bias in the ratings by the observer (eg: aggregate ratings from multiple observers).

The question has to be asked as what are the evolutionary benefits of stable personality traits. Zipser et al (2013) gave this explanation:

In highly uncertain, ever-changing environments a high degree of flexibility would mean that individuals would have to change their behavioural responses constantly according to the changes in the environment.

⁴⁰ The longer the time between repeated observations, the reliability of traits declines (Bell et al 2009). "Consequently, it may be dangerous to assume that short-term studies reflect behavioural (and by implication, personality) differences that are stable over the lifetime of individuals. This is potentially important since short-term repeatability estimates predominate in the literature, although the number of studies conducted over timeframes that may be considered more representative of natural life spans is growing..." (Boulton et al 2014).

This costly investment in a changed behavioural response profile, however, runs a high risk of not paying off as the environment might already have changed again which would render the made behavioural changes useless. In such situations, it pays to develop stable suites of behavioural responses that do best in most situations, although this brings the risk of behaving inappropriately in some... (p977) ⁴¹.

5.2. MAMMALS

A wide variety of mammals have been studied ⁴².

For example, Gosling's (1998) influential study looked at hyenas. Three experts with hyenas generated sixty potential personality traits, which were reduced to 38 general behaviour traits and six related to human interaction by two more experts (table 5.1). Four observers then used these traits with thirty-four spotted hyenas (*Crocuta crocuta*) (figure 5.1) at the University of California, Berkeley, USA. Each trait was rated for each individual from "extremely uncharacteristic" (1) to "extremely characteristic" (5) over a 26-week period.

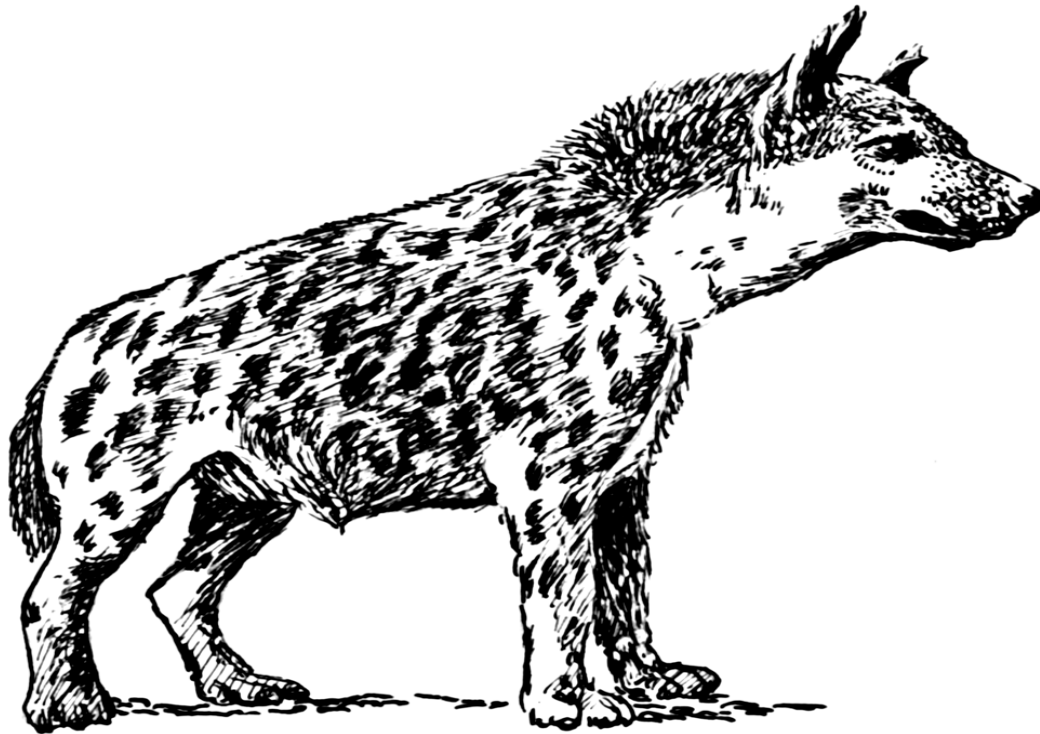
- Active, energetic: Moves about a lot, distance travelled by walking, running, climbing, or jumping. Not lethargic.
- Affiliative, companionable: Agreeable, sociable. Appears to like the company of others. Seeks out social contact with, or showing preference for, another animal; for example, playing, walking next to, or sitting with another animal.
- Aggressive: Causes harm or potential harm, high frequency of displays, threats, chasing, and biting another group member.
- Deceitful: Animal is deceitful toward humans; for example, appears to be seeking petting, but snaps at human.

(Source: Gosling 1998 appendix pp117-118)

Table 5.1 - Example of definition of traits used by Gosling (1998).

⁴¹ However, Cussen and Mench (2014) noted: "The prevalence of personality/behavioural syndromes is puzzling because it indicates that there are limits on animals' behavioural plasticity and, therefore, optimality of behaviour" (p123).

⁴² Animals behave as if individual differences are important. For example, bottlenose dolphins (*Tursiops truncatus*) produce "signature whistles", which appear to be unique to the individual animal. In playback experiments, dolphins prefer the signature whistles of familiar individuals (eg: Sayigh et al 1999) showing that they can distinguish between the calls of different individuals (Kershenbaum et al 2013). Other species can discriminate individuals based on their vocalisations, but this ability tends to use vocal cues, which are a by-product of physiological differences between individuals. "In contrast, bottlenose dolphins encode identity information in the learned frequency modulation of the signature whistles" (Kershenbaum et al 2013).



(Source: Pearson Scott Foreman; in public domain)

Figure 5.1 - Drawing of spotted hyena.

Factor analysis of the observations produced five broad personality dimensions: assertiveness, excitability, human-directed agreeableness, sociability, and curiosity (table 5.2). Gosling (1998) stated: "This dimensional structure cannot be explained primarily in terms of dominance status, sex, age, or appearance; [however]... sex differences are substantial for the assertiveness dimension but not for the other four dimensions" (p114).

Dimension	High trait examples	Low trait examples
Assertiveness (15 traits)	Aggressive; greedy; irritable	Fearful; careful
Excitability (12)	Vigilant; active; vocal	Calm; lazy
Human-directed agreeableness (7)	Obedient; flexible	Deceitful
Sociability (4)	Warm; affiliative	Cold
Curiosity (6)	Exploratory; playful; imaginative	-

(Source: Gosling 1998 table 1 p110)

Table 5.2 - Personality dimensions in hyenas.

Zipser et al (2013) investigated personality traits in nineteen adult male domestic guinea pigs (*Cavia aperea f. porcellus*) kept at a university in Germany. Three domains of personality were studied - social behaviour (eg: courtship behaviour), emotional behaviour (eg: anxiety, risk-taking), and cortisol-stress reactivity.

The following behaviour tests were used twice with an eight-week gap between them:

i) Open-field (OF) test (figure 5.2) - The individual animal is placed in the centre of a 1 m x 1 m enclosure which the researchers divided into sixteen virtual squares. Exploratory behaviour was defined as the number of squares crossed, while anxiety was the time spent in the middle during a 15-minute session.



(Source: TaoPan)

Figure 5.2 - Circular open-field test with rat.

ii) Dark-light (DL) test - Using the same enclosure, the animal is placed inside a dark box with the door open. Anxiety was measured as the time spent in the dark box in the 15-minute session.

iii) Step-down (SD) test - The animal is placed on a platform 235 mm above the ground, and risk-taking is measured by the willingness to climb down during a seven-minute period.

iv) Male-female interaction (MF) test - A male is placed in an enclosure with an unfamiliar female, and the courtship and sexual behaviour of the former is measured over fifteen minutes.

v) Cortisol reactivity (CR) test - The individual is placed in an unfamiliar environment for two hours, and changes in their cortisol level (ie: measure of stress) is calculated from blood samples taken at the beginning and end of the session.

The actual behaviour shown by the animals in each test was less important than the consistency of the behaviour across the two time points.

No stability of behaviour was found over the eight-week period in the OF, DL, and SD tests, but there was stability in the MF test. For example, males who initiated courtship and sexual behaviour early in the test did so on both occasions. Cortisol reactivity was highly stable between both CR tests. This study provided some support for animal personality traits.

5.3. PRIMATES

Freeman and Gosling (2010) found 210 relevant articles on primate personality in their literature review ⁴³. The most common animal studied was the rhesus monkey followed by chimpanzees. Only 28 (7%) of 394 primate species had been studied. Two main methods were used (as with studying non-primates) - behaviour coding (observation and coding of behaviour) and trait rating (those familiar with animals rate them on different traits). Table 5.3 summarises the main advantages and disadvantages of the two methods.

METHOD	ADVANTAGES	DISADVANTAGES
Behaviour coding	<ul style="list-style-type: none"> • Less subjective than trait rating. • Better for comparison between animals. 	<ul style="list-style-type: none"> • Time-consuming. • Risk of observer bias.
Trait rating	<ul style="list-style-type: none"> • Faster than behaviour coding. • Often uses years of experience with animals. 	<ul style="list-style-type: none"> • Subjective judgment. • Difficult to compare animals as raters may interpret traits differently.

(After Freeman and Gosling 2010 figure 3 p658)

Table 5.3 - Main advantages and disadvantages of two methods of personality assessment.

Freeman and Gosling (2010) synthesised the different personality dimensions to produce fourteen broad categories ⁴⁴. Sociability ⁴⁵, confidence/aggression ⁴⁶, and

⁴³ 70% of the studies were conducted in laboratory settings (Freeman and Gosling 2010).

⁴⁴ The most reliable dimensions were dominance and extraversion.

⁴⁵ In 69 studies.

fearfulness⁴⁷ were the most common dimensions studied/found. However, the definitions of these dimensions did vary between studies. For example, one study defined fearfulness as "a reaction, generally excessive, to potential or actual threats", while another study used the definition: "fear grins; retreats readily from others or from outside disturbances" (Freeman and Gosling 2010 p661)⁴⁸.

Concentrating on individual species, Stevenson-Hinde et al (1980) is a key study in the history of personality assessment in primates⁴⁹. Forty-six rhesus monkeys were assessed by two observers, which produced three major personality dimensions: confidence, excitability, and sociability. While King and Figuerado (1997) distinguished six dimensions of personality in chimpanzees - dominance, neuroticism, extraversion, openness, agreeableness, and conscientiousness. Of these, Weiss et al (2006) did not find openness and conscientiousness among orang-utans, but labelled a unique dimension "intellect" to cover them. This gave five dimensions of personality.

Weiss et al (2012) asserted four reasons why the personality dimensions in chimpanzees and orang-utans are real rather than products of the observers:

i) Inter-observer reliability - The individual animals are rated the same by independent observers.

ii) Reliability - The ratings are consistent over time.

iii) Generalisable - The dimensions have been found in different populations of animals.

iv) Heritability - Personality dimensions show patterns in genetic relatives.

Weiss et al (2012) stated: "There is thus little doubt that personality ratings assess real characteristics of individual animals. However, this does

⁴⁶ In 67 studies.

⁴⁷ In 45 studies.

⁴⁸ The validity of personality assessment is whether the method used measures what it claims to measure. Freeman and Gosling (2010) concluded: "Overall, the validity data present a somewhat confusing picture. The validity findings in primate personality literature indicate that there are some traits which are well validated, such as extraversion in gorillas and chimpanzees and excitable in stump-tailed macaques; however, there are other traits where the definition may need to be refined or assessed using behaviours that fit more tightly with the rating definition (eg: eccentric or depressed in chimpanzees)" (p667).

⁴⁹ Crawford (1938) is seen as the first attempt to measure personality in chimpanzees. It was in the 1980s that interest in non-human primate personality took off (Freeman and Gosling 2010).

not rule out the possibility that the striking similarities between human personality dimensions, on the one hand, and those of chimpanzees or orang-utans, on the other, are at least partially products of anthropomorphic projections" (p1356). Weiss et al (2012) sought to show that this latter point was not the case by analysing potential biases of observers (eg: that certain characteristics go together like active and friendly).

Three samples of animals were used - 202 chimpanzees in US and Australian zoos, 155 chimpanzees in zoos and research centres in Japan, and 174 orang-utans in various zoos. Each individual was rated on forty-three personality traits by up to eight observers (employees, researchers, or volunteers).

Weiss et al (2012) used various statistical techniques to establish if the ratings were based on assumptions rather than actual observations. Usually, a mean score is calculated for a trait from all the observers, but this does not remove rater individual differences (and assumptions). One technique used by Weiss et al (2012) concentrated on the individual observer and their average rating across all animals for the particular trait, which should remove rater effects. Personality dimensions using this technique were similar to previous studies using the standard technique. Weiss et al (2012) concluded:

These findings strongly rule out the possibility that similarities between the personalities of humans and great apes derived via ratings are anthropomorphic projections. Instead, they suggest that Goodall's (1990) impressions of the human-like personalities of the chimpanzees she studied reflected the chimpanzees' individual behavioural differences. Naturally, researchers should remain leery of attributing human-like personality traits such as 'thoughtlessness' to invertebrates or other distantly related species (Hebb 1946). However, researchers should also avoid engaging in 'anthropodenial' (de Waal 2009), that is, rejecting, without evidence, and even in the face of contradictory evidence, the possibility that the genetic similarity of closely related species may be expressed in behavioural similarities (p1362).

The personality of gorillas has been rated on four dimensions (used for human personality) - dominant, extravert, fearful (neurotic), and understanding (agreeableness) (Gold and Maple 1994)⁵⁰.

Weiss et al (2013) studied the data on 283 captive western lowland gorillas (*Gorilla gorilla gorilla*) in

⁵⁰ The existence of "human-like" personality traits in gorillas is seen as logical from an evolutionary point of view as gorillas and humans shared a common ancestor around ten million years ago (Weiss et al 2013).

North America, whose personalities had been rated in 1993 on the Gorilla Behaviour Index (GBI) (Gold and Marple 1994) (table 5.4) by their keepers. This has 25 behavioural adjectives (eg: "Action: moves a lot") rated from 1 (weak description) to 5 (strong description).

- Sociable - seeks companionship of others.
- Playful - initiates play and joins in when play is solicited.
- Motherly - provides a warm, receptive, secure base.
- Effective - gets own way, can control others.
- Irritable - reacts negatively with little provocation.

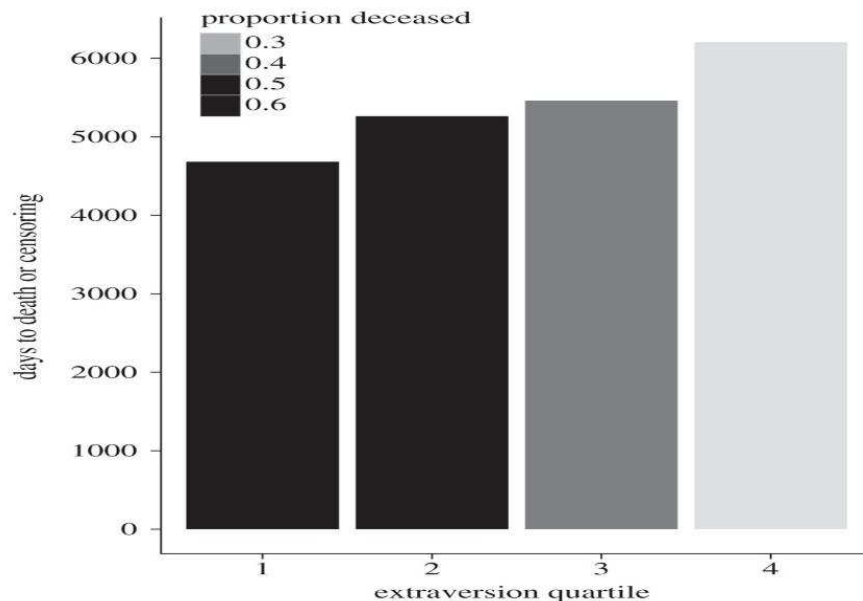
(Source: Weiss et al 2013 table S1)

Table 5.4 - Items from GBI.

More extravert gorillas (highest quartile) survived longer than the most introvert ones as assessed by the 18-year follow-up (119 individuals had died since 1993) (figure 5.3). The other personality dimensions had no relationship to survival. Why might extraversion be important to longevity? The authors made the following suggestions:

First, like rhesus macaque sociability, gorilla extraversion could be a biomarker for differences in the functioning of the immune system. Second, gorilla extraversion could be related to stronger social ties and support that, as in humans, buffer individuals from the effects of environmental stressors. Evidence consistent with this includes a study that showed an association between extraversion and higher rates of affiliation in a sub-sample of these gorillas. Another possibility is that low extraversion could be linked to cardiovascular disease, which is the primary cause of mortality in captive gorillas (Weiss et al 2013 p4).

This study depends on the accuracy of the ratings of personality in 1993. Furthermore, the reason for death was not investigated. Also, the authors admitted that they could not "conclusively rule out the possibility that the association between extraversion and longevity may be confounded by characteristics of the gorillas' enclosure or social groups. For example, it may be that gorillas who were housed in small social groups appeared to be lower in extraversion and that these small social groups led to poorer health" (Weiss et al 2013 p4).



(Weiss et al 2013 figure 1)

Figure 5.3 - Unadjusted days to death or censoring for quartiles of extraversion.

5.4. BIRDS

In humans, personality has been linked to attention bias. For example, anxious individuals attend more quickly to certain stimuli and/or are slower to disengage their attention from such stimuli. "Evolutionarily, such biases are selected for because the fitness cost of failing to attend to potentially important environmental stimuli is much greater than the cost of expending energy attending to benign stimuli" (Cussen and Mench 2014 p124).

Cussen and Mench (2014) investigated this relationship with twenty human-reared captive orange-winged Amazon parrots (*Amazona amazonica*) (figure 5.4) at a university in California, USA. Each bird was rated on thirty-six personality traits and four physical traits from 0-7 by two observers independently, and then again one year later ⁵¹.

⁵¹ This was a subjective assessment of personality.



(Source: DickDaniels <http://carolinabirds.org/>)

Figure 5.4 - Orange-winged Amazon parrot.

Factor analysis of the ratings produced two scales⁵² - "neuroticism"⁵³ and "extraversion"⁵⁴ (which were reliable over time).

Attention bias was tested by offering the parrot a choice of four containers (of which one had food inside)⁵⁵. The parrot had learned to touch a container lid to signal their choice, and the trainer would say "no" until a correct choice was made or 120 seconds passed. A failure to make any choice was classed as a "balk" trial, while making an incorrect choice(s) only was an "error" trial. Twelve parrots performed the trial individually in the presence of the trainer or an unfamiliar human/observer.

Parrots rated as higher on the neuroticism scale showed greater attention bias. That is, a poorer

⁵² Cussen and Mench (2014) pointed out the importance of personality dimensions rather than dichotomous variables (eg: bold/shy) as the latter "may overlook important consequences of personality, since actual position along the continuum can affect fitness under varying environmental conditions... For example, birds at extreme ends of the bold-shy continuum are less behaviourally flexible and have greater variability in survival in the wild than intermediate conspecifics" (p127).

⁵³ Includes 11 traits - eg: aggressive, fearful, not sociable.

⁵⁴ Includes eight traits - eg: active, bold, not lazy.

⁵⁵ Known as Hamilton search task.

performance (more balks and errors) in the presence of the unfamiliar human than the trainer. Despite being human-reared, the parrots still take time to habituate to a new human. Cussen and Mench (2014) concluded that their findings "indicate that high neuroticism individuals cannot disengage their attention from the observer to perform the task at all or, if they do, they take longer to find the food reward or fail to find the food reward. We interpret this as indicating that those individuals had an attention bias for threat..." (p129). It may be that attention bias (ie: paying attention to stranger) and high neuroticism are evolutionarily beneficial in high-threat environments (Cussen and Mench 2014).

5.5. APPENDIX 5A - BOLDNESS

There is an issue over where boldness is tested - ie: in the laboratory or in the wild.

For example, Wilson and McLaughlin (2007) found similar levels of exploration and boldness in individual brook charr (*Salvelinus fontinalis*) when tested in laboratory and in natural environment. But testing free-ranging individuals in the laboratory might involve a sampling bias (ie: higher risk-takers more likely to be caught) (Dammhahn and Almeling 2012).

In terms of tests in the wild, Garamszegi et al (2009) studied exploration, boldness, and aggressiveness in collared flycatchers (*Ficedula hypoleuca*), for example.

Dammhahn and Almeling (2012) found a positive correlation between risk-taking in a foraging task and boldness towards a novel object in the wild among grey mouse lemurs (*Microcebus murinus*) in dry deciduous forest (Kirindy) Madagascar in 2008 and 2010.

Risk-taking in foraging was tested by food placed on a small platform 1.5 metres off the ground (low-risk; LR) or on the ground (high-risk of ground predators like snakes or carnivores; HR). The platforms were left in different sites and for several nights with video cameras to aid identification of individuals. Individuals were rated for behaviours like how quickly they approached the platform and time spent there.

The novel object test involved placing the trapped individual in the vicinity of a plastic toy car and seeing if or how quickly they approached it.

Twenty-two individuals were scored on both tests. Individuals rated as bolder were quicker to approach the HR platform and spent longer feeding than low bold ones, and were more likely to approach the novel object in the other test. For example, the speed to contact novel object was significantly positively correlated to speed to approach HR platform in 2008 study (Spearman rank

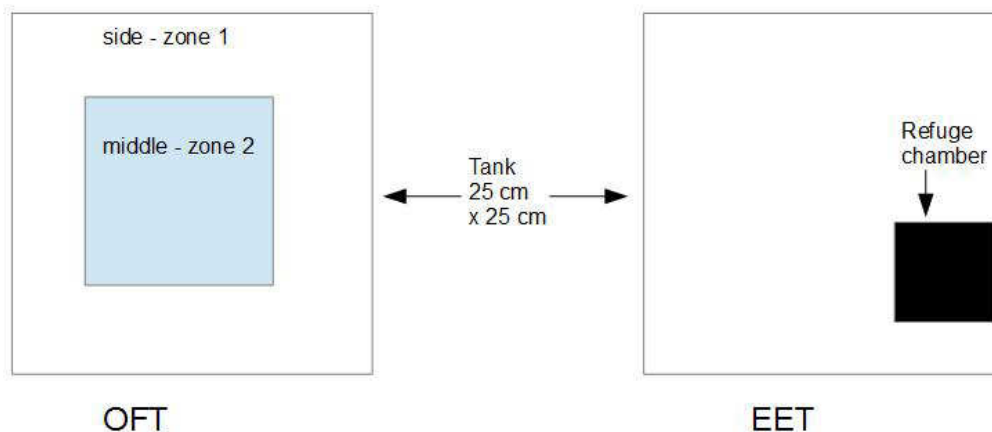
correlation; $r = 0.72$; $N = 11$; $p = 0.013$).

Boulton et al (2014) used a short time interval of four days and a longer one of 56 days in their experiments on boldness with captive-bred tropical freshwater fish (sheepshead swordtail; *Xiphophorus birchmanni*)⁵⁶. Each individual was tested in the open field trial (OFT) and in the emergence and exploration trial (EET) (table 5.5).

BASELINE	4 DAYS LATER	56 DAYS LATER
OFT	OFT	OFT
EET	EET	EET

Table 5.5 - Study design of Boulton et al (2014).

In the OFT, an individual is placed in an empty tank, and the time spent in the middle (as opposed to the side) during five minutes is used as a measure of boldness. In the EET, the fish is placed in a refuge chamber in the tank, and whether they leave the refuge is recorded (figure 5.5). Boldness is leaving the refuge and in quicker time (during 5 minutes of the trial).



(After Boulton et al 2014 figure 1)

Figure 5.5 - Aerial view of tanks in two trials.

There was consistency in rating of boldness across both types of trials (columns in table 5.5), and over the short and long time periods (rows in table 5.5).

⁵⁶ The average lifespan in the laboratory was 450 days (Boulton et al 2014).

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