PSYCHOLOGY MISCELLANY

No.36 - June 2012

Different Animal Behaviours

Kevin Brewer

Kevin Brewer BSocSc, MSc

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.
     A complete listing of his writings at http://kmbpsychology.jottit.com.

CONTENTS

1. REFLECTIONS ON ANIMAL COGNITION AND INTELLIGENCE WITH REFERENCE TO TORTOISES

1.1. INTELLIGENT BEHAVIOUR BY TORTOISES

Studies of non-human animal cognition and intelligence have looked at primates, particularly chimpanzees, other mammals (especially rats), and birds finding that these animals are able to show intelligent behaviour in different ways [1]. Reptiles, however, have been viewed as limited in intelligence until recent studies with tortoises. Here are three examples of abilities shown in experiments.

1. Wilkinson et al (2007) tested a male red-footed tortoise (Geochelone carbonaria) (figure 1.1) [2] called "Moses" on a maze traditionally used with rats. The animal is placed in the middle of eight radiating arms (20cm long and 10cm wide) (figure 1.2), each with food (pieces of strawberry) at the end [3]. Training involved making the food visible at the end of each arm from the central platform, whereas during testing the food was hidden at the end of each arm.

There were 33 trials where at least eight choices were made. Correct choices were defined as "entering an arm that had not been previously entered". In 18 trials Moses visited all eight arms successfully. Overall, his performance was better than chance (mean correct arms visited = 5.88 vs 5.3 chance; p<0.01), but less efficient than that of rats, partly due to his slowness of movement around the maze. This meant that he did not complete all eight arms in the allocated time of 30 minutes.

The ability to retrieve the food in each arm without revisiting empty arms is a measure of "cognitive map" [4].

---

[1] In the discussion about the intelligence of non-human animals the focus is usually on the intellectual abilities of a particular species. But the level of intelligence will vary between individuals within a species (appendix 1A).

[2] Red-footed tortoises are solitary animals that live at the edge of Central and South American tropical forests.

[3] Originally developed for use with rats by Olton and Samuelson (1976).

[4] "Cognitive maps" and spatial learning are linked to the area of the brain called the hippocampus,

Earlier studies had found that chelonia (turtles, tortoises, and terrapins) could learn simple mazes (probably by learning to make a sequence of turns rather than spatial learning).

(Source: In public domain)

Figure 1.1 - Red-footed tortoise.

Assessing whether food odour was aiding navigation of the maze was done by placing food in four arms randomly on some trials. Moses entered arms without food showing that odour was not a cue. To check for the use of odour trails, four arms were baited with food and Moses was allowed to find the food. Then he was removed from the maze and the other four arms were baited. There was no evidence of odour trails being used.
"Landmarks" outside the maze, like shelving, a poster on the wall, and a door, may aid in the navigation of the maze. If these "landmarks" are obscured, the tortoise used a different strategy of visiting the arm next to the one just left [5]. This is evidence of

which retiles lack (Wilkinson et al 2007).
[5] Collecting patchily distributed resources is sometimes called the "travelling salesman problem" (Lawlor et al 1985) (shortest route that visits all locations). One strategy for solving this problem is the nearest-neighbour rule (ie: visit nearest neighbour with food of current position). Lihoreau et al (2012) placed six artificial flowers around a large room for bumble-bees (Bombus terrestris) to visit. The routes of the individual bees were mapped. The bees reduced the total flight distance to visit all the flowers with each trial (from a mean of 6541 cm to 3840 cm). They used the nearest-neighbour strategy on no more than chance occasions, and preferred to fly the shortest possible distance either in a

flexibility of behaviour (appendix 1B), which is a key
sign of intelligence (Hecht 2011).
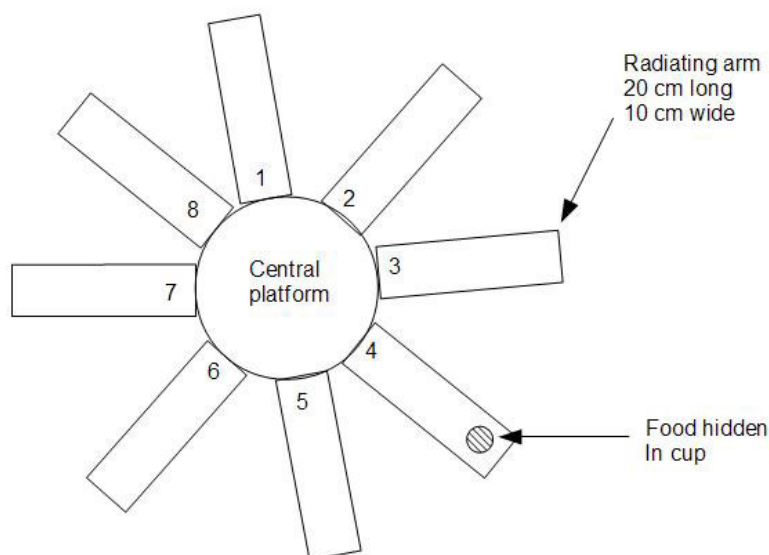
Figure 1.2 - Eight-arm maze.

     2. Wilkinson et al (2010a) found evidence of gaze
following, which is the "ability of an animal to orient
its gaze direction to that of another organism" (p765) [6].
Eight captive-bred tortoise were used, including "Moses".
     One tortoise's attention is gained with a laser
pointer on a screen (demonstrator animal), while a second
tortoise (observer animal) cannot see the laser pointer,
only the first tortoise (figure 1.3). Gaze following
occurs where the second tortoise looks in a particular
direction because the first tortoise is looking that way
(defined as head orientation in direction in five seconds
following demonstrator looking).
     At the beginning of the experimenters showed that
tortoises do not respond to the laser pointer, then they
were trained to do so. In the experimental condition, the
observer tortoise gaze followed the demonstrator tortoise
in 60% of trials. This is significantly more than in the
control conditions (10% of less of trials). One control
had a demonstrator but no laser pointer, while another
had no demonstrator but a laser pointer. Laser pointers

clockwise or anti-clockwise sequence.
[6] Gaze following has been studied in terms of following the gaze of members of the same species or
that of humans. Recent work has included some bird species (appendix 1C).

of different colours were used to stop habituation by the demonstrator tortoise.

Experimental condition

Laser pointer → screen

Demonstrator tortoise   Able to see   Observer tortoise

Control 1 – no demonstrator tortoise

Laser pointer →

Observer tortoise

Control 2 – no laser pointer

Demonstrator tortoise   Observer tortoise
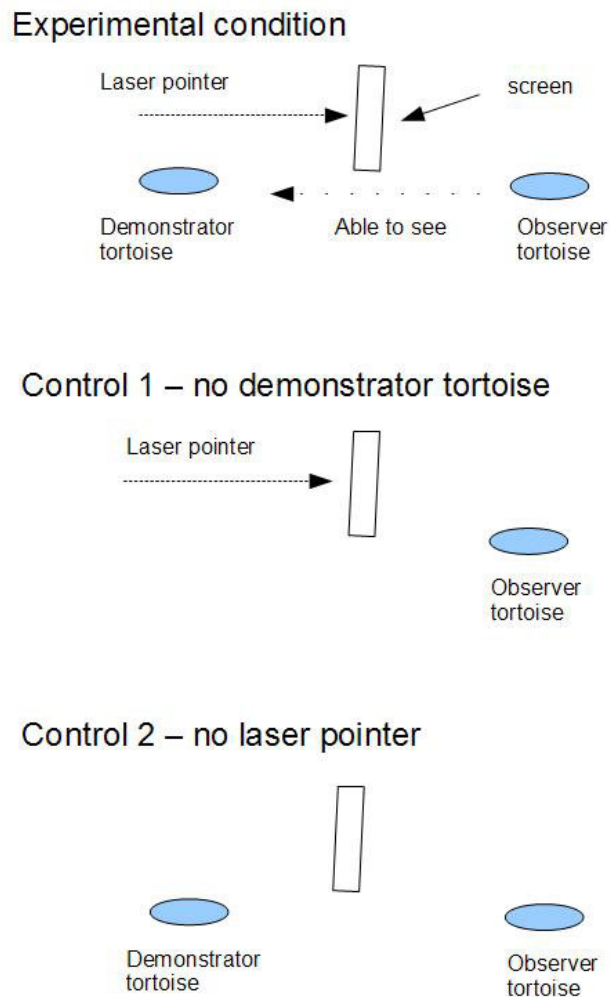
(Based on figure 1 p767 Wilkinson et al 2010a)

Figure 1.3 - The experimental set-up in Wilkinson et al (2010a).

3. Wilkinson et al (2010b) developed this research further and found social learning (appendix 1D) by tortoises. A tortoise watching another go behind a screen and find food will copy that behaviour given the opportunity (figure 1.4).
The same eight tortoises as above were studied. In the control condition with no model/demonstrator tortoise, no tortoise found food behind the screen (in 48 trials). But food was found in 29 of 48 trials when a model had been observed beforehand.

Food

Screen
50cm long

Path of
tortoise

Demonstrator
tortoise

Transparent
screen

Observer
tortoise
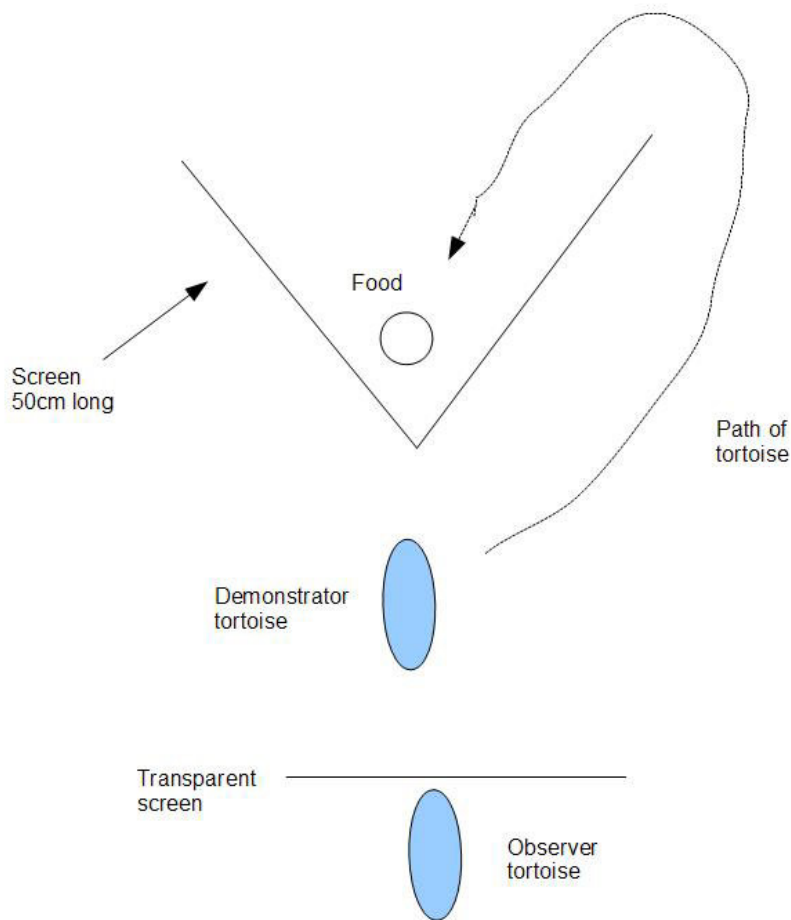
(Based on figure 1 p615 Wilkinson et al 2010b)

Figure 1.4 - The experimental set-up in Wilkinson et al (2010b).

These findings challenge the hypothesis that social learning occurs in social animals only. An alternative explanation is that an animal with cognitive capacity to learn will learn in a variety of different ways (eg: social learning, trial and error) (Heyes 2003).

Finding intelligent behaviour by tortoises has an evolutionary basis as tortoises receive no parental care after hatching. Thus survival for these individuals who evolved intelligence (Hecht 2011).

It is important in experiments that the room temperature is similar to that the reptiles are used to (eg: 27-29°C). They are cold-blooded animals and will be very sluggish at lower temperatures. Previous research

that found little evidence of intelligent behaviour among reptiles may have had the temperature too low (Hecht 2011).

1.2. APPENDIX 1A - CLEVER INDIVIDUAL ANIMALS

Some individual animals in a species are cleverer than others. For example, researchers found three cleverer apes from among thirty living in captivity in Leipzig and seventeen chimpanzees out of 106 in two African sanctuaries. Of the latter group, a chimpanzee called "Natasha" stood out (Marshall 2012).

Two factors that are common to high intelligence individual animals are age (adults cleverer than juveniles) and exposure to/raised by humans. "Natasha" was the same on these as other less intelligent chimpanzees at the sanctuaries, but her "social intelligence" (eg: observational learning; shared problem-solving) was higher (Marshall 2012) [7].

Individual animals are often studied in artificial situations, like captivity and/or being raised by humans, and then assumptions are made about the whole species. These "animal einsteins" (Marshall 2012) include a bonobo who uses sign language to communicate ("Kanzi"), and a parrot who understood concepts and numbers ("Alex"). Unfortunately, these hot-housed individuals, and statements about the intellectual abilities of a species needs to see the behaviour among many individuals.

There is always the question of why intelligence evolved. Any behaviour will evolve if it aids survival, and allows the possessor to have more offspring. So intelligent individuals should do better in the survival stakes in tough environments in particular. Studies with birds confirm (eg: Roth et al 2010 [8]) and challenge this statement. In the latter case, great tits (Parus major) who were good at problem-solving did not obtain more food because other individuals muscled in (Marshall 2012).

However, intelligent individuals of this species may have more offspring (Marshall 2012).

---

[7] For example, Dean et al (2012) found that children could retrieve sweets from a puzzle box through working together whereas chimpanzees worked alone and failed.

[8] Animals living in harsh environments benefit from more advanced cognitive abilities. Roth et al (2010) compared hand-reared black-capped chickadees (Poecile atricaphilus) taken at ten days old from two populations in the USA - Alaska (harsh environment) and Kansas (mild environment) - on a problem-solving task. The task was to remove a lid covering a well containing food. The birds from Alaska were significantly faster at solving the problem.

1.3. APPENDIX 1B - BEHAVIOURAL FLEXIBILITY AND COGNITION

Behavioural flexibility is "the ability of an individual to change its behaviour by developing new responses to novel stimuli or altering existing responses to familiar stimuli" (Leal and Powell 2012 p28).

Leal and Powell (2012) reported evidence of behavioural flexibility in experiments with a tropical arboreal lizard (Anolis evermanni) [9] from Puerto Rico (USA) (figure 1.5). After training with the apparatus, the task was to remove a blue coloured lid from the top of a plastic well that contained food, and ignore an empty well with another coloured lid.

Four of the six lizards tested were able to dislodge the lid, which was done by biting the edge of it or using their snout as a lever. These four lizards were able to distinguish the correct coloured well that contained food, but only two showed reversal learning (ie: during training food associated with one colour lid, but placed in other well for test).

This behavioural flexibility was unexpected in a species that has no complex social structure, and whose foraging tends to be mainly sit-and-wait (Leal and Powell 2012). Vasconcelos et al (2012) challenged the findings and criticised the experimental methodology.

(Drawn using MapCreator2)

Figure 1.5 - Position of Puerto Rico.

One characteristic of intelligent behaviour is

---

[9] Called Emerald anole, Evermann's anole or small green anole. Information at reptile-database (http://reptile-database.reptarium.cz/species?genus=Anolis&species=evermanni&search_param=%28%29).

planning for the future. Such behaviour is viewed as rare among non-human animals. Osvath (2009) reported an interesting case of a male chimpanzee ("Santino") at Furuvik Zoo in Sweden who collected stones and concrete objects before the zoo opened to throw at visitors later in the day.

There are odd cases of experimental work where the cognition of animals is better than humans. One example is chimpanzees and numerical recollection in a "limited-hold memory task". The numbers 1-9 are shown on a touch-screen in a random organisation, and the task is to touch the part of the screen in numerical order. But the numbers are only presented for a brief period, and recall of the spatial organisation is required. The time period for showing the numbers was 650, 430, and 210 ms.

Inoue and Matsuzawa (2007) reported the results from tests comparing two trained humans and chimpanzees at the Primate Research Institute, Kyoto University, Japan. Using five numbers, the humans' performance declined as the numbers were presented for a shorter time (80% correct at 650 ms to 40% at 210 ms). One of the chimpanzees, a mother, "Ai" showed a similar decline (55% to 20% correct respectively), but a young chimpanzee, "Ayumu", remained at 81% correct even at 210 ms presentation of the numbers.

Grandin (2005) argued that specific exceptional cognitive abilities shown by some animals (eg: birds remembering thousands of cache sites) can be compared to human autistic savants who have extraordinary skills in one area only (eg: music, mathematics).

Vallortigara et al (2008) preferred to see these abilities as adaptive specialisations. If the animals are behaving like autistic savants then the specific cognitive ability will be at the expense of other abilities. But Clark's nutcrackers, for example, who can recall many cache sites "do not show any impairments in other cognitive domains" (Vallortigara et al 2008).

1.4. APPENDIX 1C - GAZE FOLLOWING IN MOSTLY BIRDS

Two levels of gaze following have been distinguished (Gomez 2005). Gaze following into distant space (ie: looking in the direction of the other individual's gaze) and geometrical gaze following (ie: looking behind a barrier after seeing the other individual look there). The latter is viewed as a "more advanced activity".

Loretto et al (2010) found that Northern bald ibises (Geronticus eremita) (figure 1.6) in Austria were able to do the former but not the latter. In experiment 1 on gaze following into distant space, a demonstrator bird looked

upwards at a laser dot that the observer bird could not
see. Over 60% of observer birds looked upwards within ten
seconds of the demonstrator doing so compared to less
than 10% in the control condition (no demonstrator bird).
        Experiment 2 tested geometrical gaze following. A
demonstrator bird looked behind a barrier at food in the
presence of an observer bird. Most of the observer birds
looked at the barrier (and more than in the control), but
less than 20% of them walked around the barrier when
given the opportunity.

(Source: Naumann "Natural History of Birds of Central Europe"; in public domain)

Figure 1.6 - Drawing of Northern bald ibises.

        Bugnyar et al (2004) reported that seven hand-raised
ravens (Corvus corex) could follow the gaze of humans in

both types of experiment. Each bird participated in all four conditions - human looks up versus looks at bird (control), and human looks behind a wooden barrier versus looks away (control). The ravens followed the human's gaze in one-third to one-half of trials. Bugnyar et al (2004) admitted: "Although our results support the idea that ravens may understand something about the visual activities of others, the degree to which they attribute mental significance to the visual behaviour of others remains an open question" (p1334).

Using hand-reared birds is easier for researchers performing experiments, but such animals and their behaviour are not necessarily representative of wild members of the species, and care should be taken in generalising the findings. Leavens et al (2010) gave the example of pointing by chimpanzees which is extremely rare in wild chimpanzees, more common in captive ones, and found in all home-raised and language-trained individuals. Different conclusions about pointing will be drawn depending on the sample studied.

Jaime et al (2009) found that hatchlings (1-3 days old) of Northern bobwhite quail (Colinus virginianus) (figure 1.7) could track the direction of human gaze, but only after experience with human faces.
The birds were randomised to one of five conditions:

i) Direct Gaze condition - a human is looking down at one of two identical areas broadcasting bobwhite maternal calls (figure 1.8).

ii) Gaze Follow condition - a human moves their gaze towards one of the two areas.

iii) Masked Gaze Follow condition - as condition (ii) but the human is wearing a mask that hides their gaze (control condition for ii). Birds in this condition were familiar with human faces, however.

iv) Deprived Face Experience condition - as condition (ii) but using hatchlings who had no previous experience with human faces (ie: reared by humans wearing masks).

v) Control condition - no human present in experiment.

The behaviour of the birds was measured by their choice of one area of the arena within five minutes of experiment beginning.
In the Direct Gaze and the Gaze Follow conditions, the birds significantly preferred the non-gazed area, while the other conditions had no difference. This is evidence of gaze following but in the form of aversion to

(Source: Pearson "Birds of America"; in public domain)

Figure 1.7 - Drawing of adult Northern bobwhite quail.

gaze. There are survival benefits to responding to gaze
in this way. For example, Ristau (1991) found that when a
human looked at the nest of piping and Wilson's plovers,
the mother feigned injury in the line of sight of the
viewer but away from the nest.
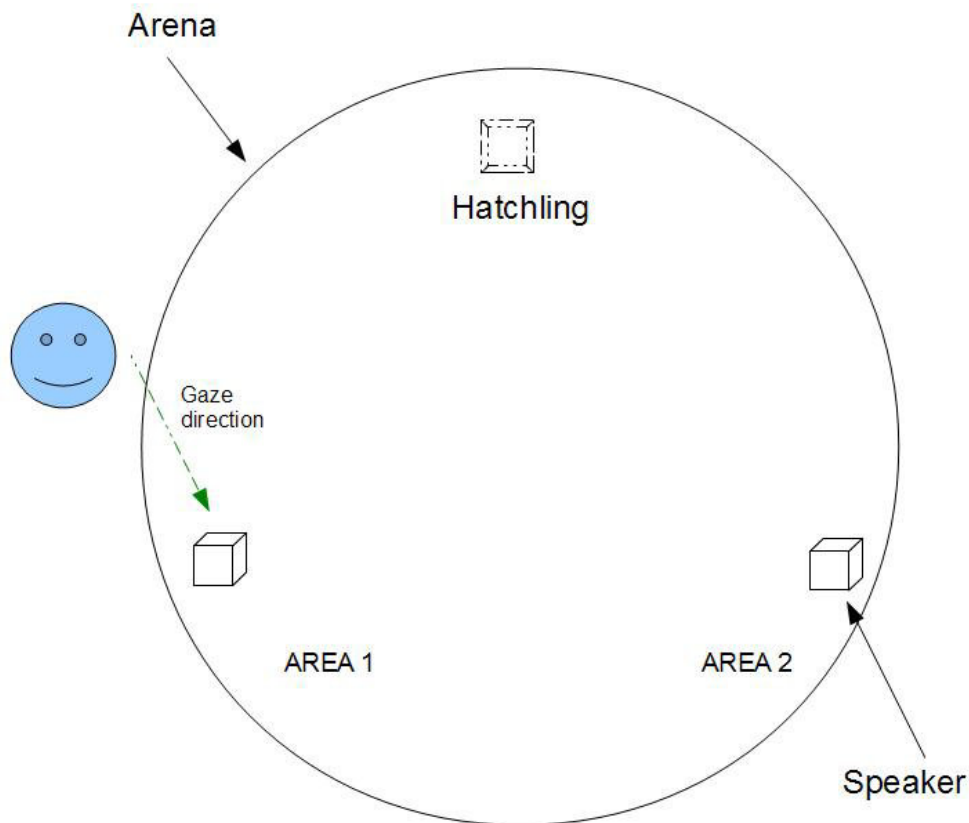
Figure 1.8 - Drawing of Direct Gaze condition.

        Gaze following of own species is influenced by
factors like facial expression, and the relationship
between the animals. In the former case, for example,
gaze following is enhanced in long-tailed macaques when
the gazer is displaying fear (Goosens et al 2008).
Shepherd et al (2006) found that low-status rhesus
monkeys follow the gaze of other individuals whilst high-
status individuals only do so with other high-status
individuals.
        Among crested macaques (Macaca nigra) at a zoo in
England, individuals were quicker to react to the gaze
cues of "friends" (defined based on time spent grooming)
than non-friends, but there was no difference in how
often the gaze was followed (Micheletta and Waller 2012).
In a pair of animals, one (informer) could seen the
experimenter holding food and the other (responder) could
not.

1.5. APPENDIX 1D - SOCIAL LEARNING

Social learning is "any incidence in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals or their products" (Brown and Laland 2003 p280-281).

Davis and Burghardt (2011) outlined eight different types of social learning:

i) Contagion/contagious behaviour - A behaviour is automatically triggered by other individuals performing that behaviour.

ii) Social facilitation/social enhancement - The mere presence of another individual causes arousal in the observer, who subsequently is more likely to come into contact with the stimulus for a behaviour. Or "the behaviour of one individual induces an identical behaviour in another individual and the latter then learns something via the expression of this behaviour, for instance, it learns about the consequences of producing behaviour in that context" (Brown and Laland 2003 p281).

iii) Local enhancement - The behaviour of an individual attracts the attention of an observer.

iv) Stimulus enhancement - The behaviour of one animal attracts the attention of an observer to a particular stimulus.

v) Observational conditioning - The behaviour of one animal attracts the attention of an observer to a stimulus and its reinforcement.

vi) Goal emulation - An observer learns the goal to pursue (not the behaviour) from a model.

vii) Copying - An observer copies the behaviour of a model.

viii) True imitation - An observer copies a behaviour of a model that they have never done before.

Brown and Laland (2003) added guided learning or exposure, which is defined as "by following or being with a knowledgeable animal, an individual is exposed to similar features of the environment and comes to learn the same behaviour" (p281).

Davis and Burghardt (2011) tested four Florida Red-bellied Cooters (turtles) (Pseudomys nelsoni) in experiments on three different types of social learning.

a) Stimulus enhancement was tested by observing a trained turtle (model) approach a white bottle (which contained food pellets) instead of a black one and knock it over. The bottles were placed on bricks above the water in a tank, and to reach them involved climbing out of the water.

b) Goal emulation was tested by observing a model dislodge the bottle to gain the food, either by biting it, pushing it with nose, or swiping with foot.

c) Copying was tested by observing a model dislodge the bottle in a particular way (eg: swiping with right or left foot).

All four turtles showed evidence of stimulus enhancement, but not the other two types of social learning. In 46 trials, the same bottle was approached as the model had approached on 41 of them. Davis and Burghardt (2011) admitted that this behaviour may actually be an example of observational conditioning as the model was seen to gain food which the observers did not (ie: no reinforcement for them).

This set of experiments involved turtles hatched and raised in the laboratory, and there was detailed training of model and observer which makes the situation different to the natural environment. Thus the experiments had low ecological validity.

Brown and Laland (2003) gave examples of different types of social learning among fishes in relation to:

(i) Anti-predator behaviour - learning to identify predators, and make appropriate anti-predator responses. For example, Brown and Laland (2002) showed that naive fish would copy the escape route of a demonstrator fish in response to an artificial predator, and this was more efficient (with the demonstrator present or absent) than a control group (no demonstrator).

(ii) Migration and orientation - learning routes to food, resting or mating sites. For example, Laland and Williams (1997) had observer guppies watch a demonstrator fish take a route to feed, and the fish copied this route when the demonstrator was removed and an alternative route was offered. This is guided learning which is typical of coral reef fish.

(iii) Foraging - eg: local enhancement is observed in behaviour called "forage area copying" (Barnard and Sibley 1981) where one fish finding a patch of food cues the rest of the shoal to follow it. While Anthouard (1987) taught a new behaviour to European sea bass through observation of a model pressing a lever to

receive food.

(iv) Mate choice - eg: experiments with the "mate choice copying" paradigm (eg: guppies; Dugatkin 1992). A female observer, for example, watches another female choose to mate with one of two males. When given the chance, the observer prefers to mate with the male previously chosen. The chosen male is assumed to be of better quality and that is what the observer learns.

1.6. REFERENCES

Anthouard, M (1987) A study of social transmission in juvenile Dicentrarchus labrax (pisces, serranidae) in an operant-conditioning situation Behaviour 103, 266-275

Barnard, C & Sibley, R (1981) Producers and scroungers: A general model and its application to feding flocks of house sparrows Animal Behaviour 29, 543-550

Brown, C & Laland, K.N (2002) Social learning of a novel avoidance task in the guppy, P.reticulata: Conformity and social release Animal Behaviour 64, 41-47

Brown, C & Laland, K.N (2003) Social learning in fishes: A review Fish and Fisheries 4, 280-288

Bugnyar, T et al (2004) Ravens, Corvus corax, follow gaze direction of humans around obstacles Proceedings of the Royal Society of London B 271, 1331-1336

Davis, K.M & Burghardt, G.M (2011) Turtles (Pseudomys nelsoni) learn about visual cues indicating food from experienced turtles Journal of Comparative Psychology 125, 4, 404-410

Dean, L.G et al (2012) Identification of the social and cognitive processes underlying human cumulative culture Science 335, 1114-1118

Dugatkin, L.A (1992) Sexual selection and imitation: Females copy the mate choice of others American Naturalist 139, 1384-1489

Gomez, C (2005) Species comparative studies and cognitive development Trends in Cognitive Science 9, 118-125

Goosens, B.M.A et al (2008) Gaze following in monkeys is modulated by observed facial expressions Animal Behaviour 75, 1673-1681

Grandin, T (2005) Animals in Translation New York: Scribner

Hecht, J (2011) Who are you calling slow? New Scientist 24/31 December, 44-45

Heyes, C.M (2003) Four routes to cognitive evolution Psychological Review 110, 713-727

Inoue, S & Matsuzawa, T (2007) Working memory of numerals in chimpanzees Current Biology 17, 23, R1004-R1005

Jaime, M et al (2009) Bobwhite quail (Colinus virginianus) hatchlings track the direction of human gaze. Animal Cognition 12, 4, 559-565

Laland, K.N & Williams, K (1997) Shoaling generates social learning of foraging information in guppies Animal Behaviour 53, 1161-1169

Lawlor, E.L et al (1985) The Travelling Salesman Problem: A Guided Tour of Combinatorial Optimisation Chichester: Wiley

Leal, M & Powell, B.J (2012) Behavioural flexibility and problem-solving in a tropical lizard Biology Letters 8, 28-30

Leavens, D.A et al (2010) BIZARRE chimpanzees do not represent "the chimpanzee" Behavioral and Brain Sciences 33, 2-3, 100-101

Lihoreau, M et al (2012) Bees do not use nearest-neighbour rules for optimisation of multi-location routes Biology Letters 8, 1, 13-16

Loretto, M-C et al (2010) Northern bald ibises follow others' gaze into distant space but not behind barriers Biology Letters 6, 14-17

Marshall, M (2012) Off-the-chart animal smarts New Scientist 24/3, 6-7

Micheletta, J & Waller, B.M (2012) Friendship affects gaze following in a tolerant species of macaque, Macaca nigra Animal Behaviour 83, 459-467

Olton, D.S & Samuelson, R.J (1976) Remembrance of places passed: Spatial memory in rats Journal of Experimental Psychology: Animal Behavior Processes 2, 97-116

Osvath, M (2009) Spontaneous planning for future stone throwing by a male chimpanzee Current Biology 19, 5, R190-R191

Ristau, C.A (1991) Aspects of the cognitive ethology of an injury-feigning bird, the piping plover. In Ristau, C.A (ed) Cognitive Ethology: The Minds of Other Animals Hillsdale, NJ: Erlbaum

Roth, T.C et al (2010) Learning capabilities enhanced in harsh environments: A common garden approach Proceedings of Royal Society B 277, 3187-3193

Shepherd, S.V et al (2006) Social status gates social attention in monkeys Current Biology 16, R119-120

Vallortigara, G et al (2008) Are animals autistic savants? PLoS Biology 6, 2, e42

Vasconceles, M et al (2012) On the flexibility of lizards' cognition: A comment on Leal and Powell (2011) Biology Letters 8, 42-43

Wilkinson, A et al (2007) Spatial learning and memory in the tortoise (Geochelone carbonaria) Journal of Comparative Psychology 121, 4, 412-418

Wilkinson, A et al (2010a) Gaze following in the red-footed tortoise (Geochelone carbonaria) Animal Cognition 13, 765-769

Wilkinson, A et al (2010b) Social learning in a non-social reptile (Geochelone carbonaria) Biology Letters 6, 614-616

2. ANIMAL SEX

2.1. UNCOMMON EXAMPLE

Wege et al (2011) reported the unusual observation at Trypot Beach, Marion Island, South Africa (figure 2.1) of an Antarctic fur seal pup (Artocephalus gazella) attempting to copulate with its mother. On at least three occasions in March 2010 the male pup was observed to move from suckling to attempted copulation. Some other species of seal show sexual play behaviour (eg: common seal), but these observations seemed more than that because on one occasion the pup when attempting to copulate was chased away by a young adult male. This would suggest that the pup's behaviour was interpreted as attempted copulation rather than sexual play behaviour. However, the authors argued that sexual play behaviour is common in juveniles, but has "never before been seen directed at an individual's own mother".

(Source: Photo from NASA in public domain; map produced using MapCreator2)

Figure 2.1 - Position of Marion Island and enlarged satellite photograph of island.

2.1.1. Sexual Coercion

Sexual coercion takes three main forms (Clutton-Brock and Parker 1995):

i) Forced copulation - Males being physically stronger and/or larger than females of a species allows them to copulation by force. For example, most copulations by sub-adult male orang-utans (Pongo pygmaeus) and half the copulations by adult males were observed to occur after female resistance was violently suppressed (Mitani 1985).
Forced copulation could evolve where males are not involved in raising their offspring, where there is a risk of other males mating with the female (eg: wandering males and stationary females), or male life expectancy is short (Clutton-Brock and Parker 1995).
But females may evolve strategies to combat this behaviour - eg: larger female body size to fight off males, or, as in some insects, genitalia that makes forced copulation impossible (Clutton-Brock and Parker 1995).

ii) Harassment - Repeated attempts to copulate by males has costs to the females (eg: physical injury; energy expenditure to avoid; risk of predation), which the females reduce by mating immediately. This is sometimes called "repeated courtship" - eg: male fallow deer (Dama dama) continue to court and mate with females that initially refuse (Clutton-Brock et al 1988). The cost for males is less opportunity to feed.

iii) Intimidation - Males punish females who refuse to mate, and this cost to the females makes them more likely to mate in the future. Intimidation may also be used by dominant males to stop females consorting with other males, or used more generally by males on receptive or near-receptive females. For example, captive female lowland gorillas (Gorilla gorilla) were observed to present for copulation more frequently to more aggressive males (Clutton-Brock and Parker 1995).

2.1.2. Pinnipeds

In species that are sexually dimorphic (appendix 2A), sexual aggression and coercion are a risk. In such species, the males (who are usually physically much larger than the females) are the perpetrators. This male harassment at the extreme can lead to death of females as well as to their offspring (eg: accidentally squashed during harassment). This is a cost for females, in terms of reproductive success, which produces strategies by the females to reduce this male behaviour (eg: evasion,

resistance, receptivity, gaining protection from dominant males, or grouping of females) (Chivers et al 2005).

"For many pinniped species [10], and particularly in gregarious breeders, sexual behaviour is aggressive and energetically costly for males and potentially lethal for females" (de Bruyn et al 2008 p295).

Among pinnipeds like the New Zealand sea lion (Phocarctos hookeri), male harassment manifests itself as (Chivers et al 2005):

- Detainment - chest to chest contact that stops females from moving forward.
- Lunging - thrust at female with open mouth.
- Biting.
- Charging.
- Compression of female beneath male that causes suffocation or drowning.

These behaviours occur during copulation attempts by non-dominant males, and harem capture. In the latter case, a dominant male maintains a harem of females on the beach, and aggressively recruits females to it. Other males may raid the harem, which is another source of female injury. Females can also be injured during territorial disputes between harem-owners.

Chivers et al (2005) reported, from their observations of New Zealand sea lions at Sandy Bay (southern coast) on Enderby Island (north-east Auckland Islands), New Zealand (figure 2.2), that 0.5% of breeding females die each year from such behaviours, and 84% of adult females examined had permanent scars from male bites.

Rose et al (1991) reported observations of male northern elephant seals (Mirounga angustirostris) mounting live and dead weaned pups, other sub-adults, pregnant females, dead females and dead sea lions. Most males do not mate in a breeding season because the dominant males control the harems, so it is these subordinate males who are mounting weaned pups, for example. Rose et al collected their data over five breeding seasons at Ano Nuevo State Reserve, San Mateo County, California, USA. The researchers noted that pups can look similar to adult females in body and head shape, and this might explain the behaviour.

The gregarious and aggressive nature of males can lead to inter-species breeding with closely related species as well as non-reproductive sexual advances (de

---

[10] Pinnipeds are semi-aquatic mammals including different species of seals.

Bruyn et al 2008). But de Bryun et al (2008) observed an unusual case of a young male Antarctic fur seal attempting to copulate with an adult king Penguin (Aptenodytes patagonicus) on Marion Island.

    The researchers were not sure whether the behaviour was sexual play by the seal or the excitement of predating a penguin being redirected into sexual arousal.
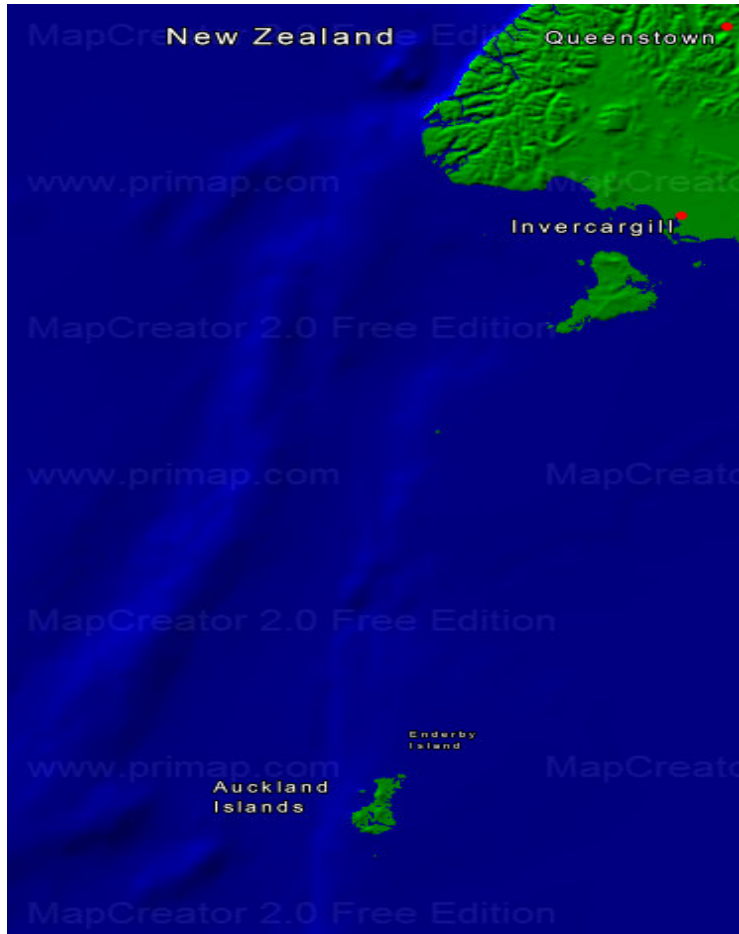
(Source: Map produced using MapCreator2)

Figure 2.2 - Position of Enderby Island.

2.2. ORAL SEX

    Tan et al (2009) reported the rare case among non-human animals of oral sex by short-nosed fruit bats (Cynopterus sphinx). The female licks the base of the already-penetrating male penis.

    Thirty pairs of tagged bats in Ornamental Chinese fan-palm trees in Yuexiu Park, Guangzhou City, southern China (figure 2.3) were observed at night over three different months in 2007. Pairs where oral sex occurred copulated for significantly longer than non-oral sex

(Drawn with MapCreator2)

Figure 2.3 - Guangzhou City.
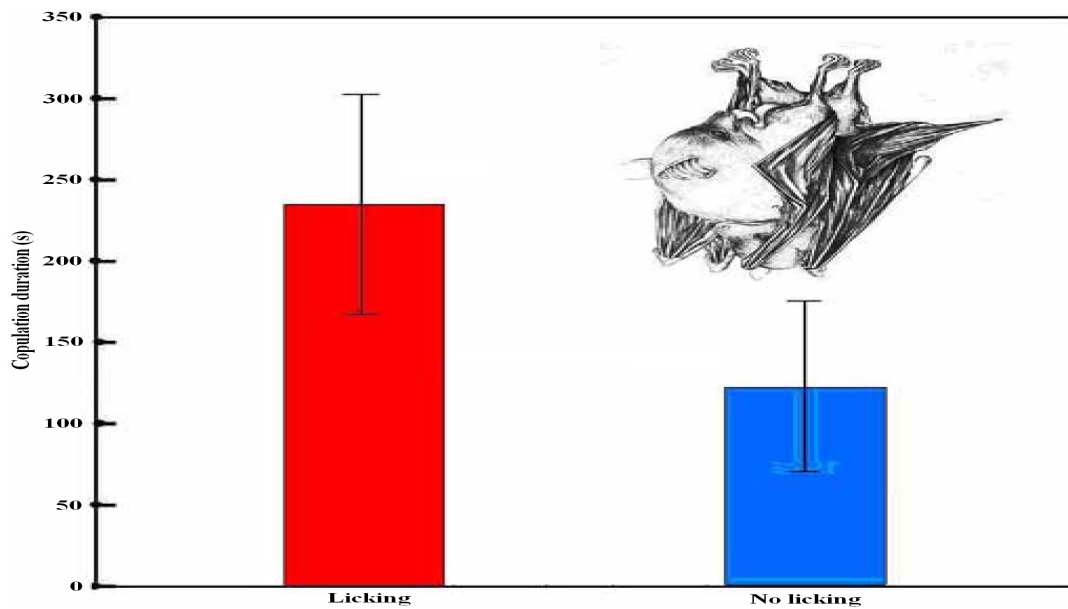
(Vignette shows a female performing fellatio, drawn by Mei Wang)

(Source: doi:10.1371/journal.pone.0007595.g003)

Figure 2.4 - Mean copulation duration based on presence of oral sex or not.

pairs (mean 220 vs 122 seconds) [11] (figure 2.4), and the length of time of oral sex significantly positively correlated with duration of copulation [12] (figure 2.5).
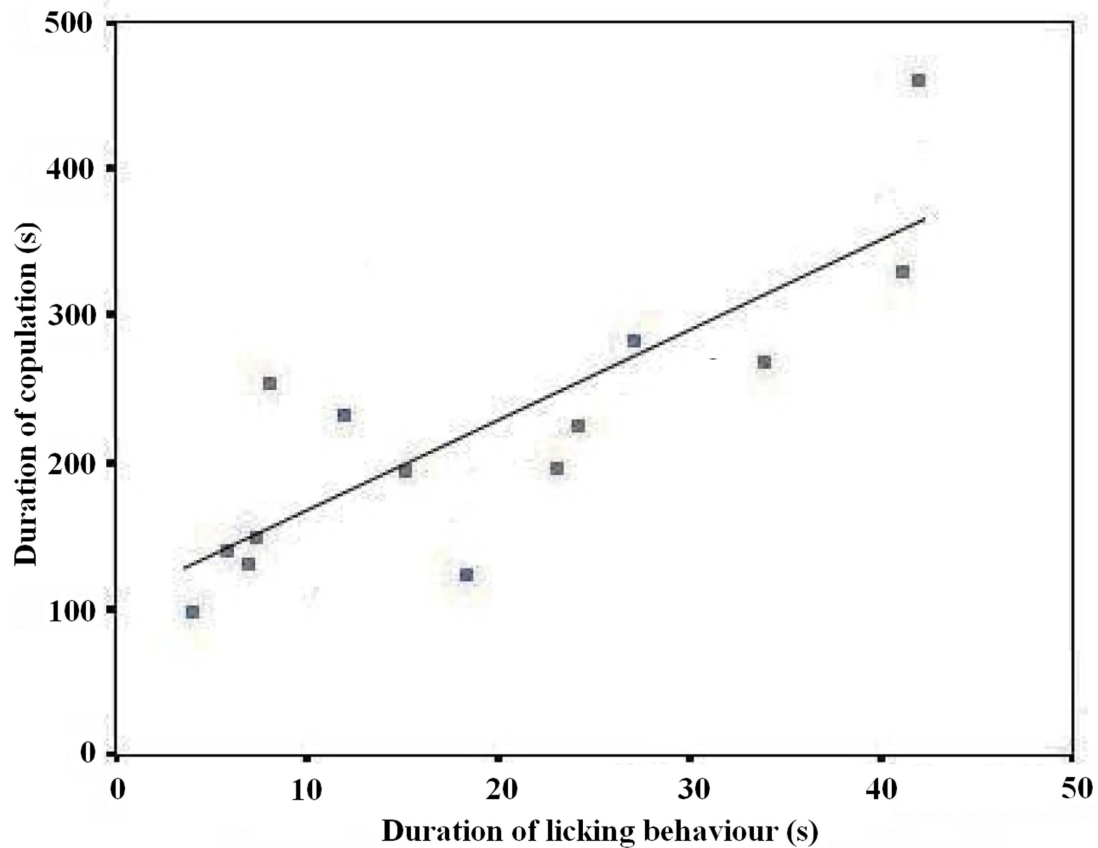
(Source: doi:10.1371/journal.pone.0007595.g003)

Figure 2.5 - Relationship between duration of copulation and length of oral sex.

Tan et al proposed four possible reasons for the evolution of such behaviour:

* It prolongs copulation which increases the opportunity for sperm to fertilise the female.
* It prolongs copulation and thereby limits the opportunity for the male to mate with other females (both in terms of time and availability of sperm).
* The saliva in the licking prevents sexually transmitted diseases.
* The female can detect chemical cues about the male in licking (eg: immune system compatibility and health).

---

[11] MannWhitney U test; $p = 0.039$.
[12] $r = 0.83$; Pearson's test; $p < 0.001$.

Observations of oral sex in other non-human animals include (Tan et al 2009):

- As play in juvenile bonobo chimpanzees.
- To increase arousal of the male in orang-utans.
- Male lemurs lick female genitals to judge whether she is in oestrous (ie: ready to mate).

2.3. APPENDIX 2A - SEXUAL DIMORPHISM

Sexual dimorphism refers to differences between the sexes of a species in body size (sexual size dimorphism) or in body parts used in fighting or courtship displays (eg: horns in males) (Logunov 2011) (figure 2.6).

(Source: user:benjamint444)

Figure 2.6 - Example of sexual dimorphism in birds (colourful male and plainer female superb fairy-wren).

Sexual dimorphism is common among spiders, where the females are usually larger than the males (figure 2.7). The differences can be very large - eg: the male ladybird spider (Eresus cinnaberinus) half the size of the female, or orb-web spider (Nephila fenestrata) where the male may be one hundred times lighter than the female (Logunov 2011).

(Source: B.Navez)

Figure 2.7 - Large female and small male Nephila inaurata.

What are the possible reasons for the large sexual size dimorphism as seen in spiders [13]?

1. Females are larger because of the physical demands of producing webs and raising offspring which males do not have to do. From an evolutionary point of view, larger females who produce more offspring (ie: higher fecundity) will be favoured by males because offspring mortality is high. Larger females will be more able to protect the young from predation, and to be effective predators themselves. Again reasons for males to favour larger females. But there are costs to becoming larger in terms of energy requirements, time to grow, and greater risk of predation (Logunov 2011).

2. Selection pressures may produce smaller males in species where males wander around looking for sedentary/stationary females. Here male reproductive

---

[13] Coddington et al (1997) is an example, with Nephila clavipes, of the debate over whether females evolved to be larger or males evolved to be smaller.

success is a "first come first served" principle
("scramble competition"). Males who reach sexual maturity
quicker will have a better chance to find females first
than males who take a longer time to mature. It is not so
much the small size that evolved, but the shorter
ontogeny (ie: shorter period between fertilised egg and
maturity) (Logunov 2011).

2.4. REFERENCES

Chivers, B.L et al (2005) Male harassment of female New Zealand sea
lions, Phocarctos hookeri: Mortality, injury, and harassment avoidance
Canadian Journal of Zoology 200, 83, 642-648

Clutton-Brock, T.H & Parker, G.A (1995) Sexual coercion in animal
societies Animal Behaviour 49, 1345-1365

Clutton-Brock, T.H et al (1988) Passing the buck: Resource defence,
lek breeding and mate choice in fallow deer Behavioural Ecology and
Sociobiology 23, 281-296

Coddington, J.A et al (1997) Giant female or dwarf male spiders?
Nature 385, 687-688

de Bruyn, P.J.N et al (2008) Sexual harassment of a king penguin by an
Antarctic fur seal Journal of Ethology 26, 295-297

Logunov, D (2011) Giant brides and dwarf grooms - sexual size
dimorphism in spiders Feedback 51, 15-18

Mitani, J.C (1985) Mating behaviour of male orang-utans in the Kutai
Reserve Animal Behaviour 33, 392-402

Rose, N.A et al (1991) Sexual behaviour of male northern elephant
seals: III. The mounting of weaned pups Behaviour 119, 3-4, 171-192

Tan, M et al (2009) Fellatio by fruit bats prolongs copulation time
PLoS ONE 4, 10, e7595 (Freely available at
http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0007595)

Wege, M et al (2011) Oedipus complex in an Antarctic fur seal pup?
Journal of Ethology 29, 505-507

3. CO-OPERATIVE AND COMMUNAL BREEDING

3.1. Co-operative breeding
3.2. Appendix 3A - "Pay-to-stay"
3.3. References

3.1. CO-OPERATIVE BREEDING

Co-operative breeding is where a non-reproductive individual (adult or sub-adult), who may or may not be genetically related, helps rear the offspring of others. For example, in bird species with demanding nestlings, the provision of food by adults as well as the parents increases the survival chances of the nestlings.

Wong and Balshine (2011) stated the key questions about co-operative breeding:

i) Why do helpers stay to help rather than disperse elsewhere to breed?

ii) Who do helpers forego breeding?

iii) Why do helpers help raise the offspring of others?

In relation to the last question, Wong and Balshine (2011) outlined four hypotheses with the example of African cichlid fish (Neolamprologus pulcher).

a) Kin selection - The helpers are genetically related to the breeders and their offspring, and helping improves the survival of the shared genes.
Studies have no found no difference in helping towards kin and non-kin in cichlids (eg: Stiver et al 2005).

b) Pay-to-stay" (appendix 3A) - Individuals help as "payment" for remaining in the territory of the breeders. Wong and Balshine (2011) pointed out that the expected prediction that lazy helpers are punished by the territory owners is not supported in all studies with cichlids.

c) Signals of prestige - Helping is a signal of reproductive fitness for future reproduction. Individuals who can afford the energy costs of helping are advertising their quality (Zahavi 1995).
From this idea, it can be predicted that the level of helping will be correlated with future reproductive opportunities, and that helpers will be more helpful in front of an audience. But these predictions have not been

directly tested with cichlids (Wong and Balshine 2011).

d) Group augmentation hypothesis - Helping enhances the group size, and this increases helper survival and thus future opportunities for reproduction (Woolfenden 1975). There is some support for the benefits to cichlids of residing in a group (Wong and Balshine 2011).

Wong and Balshine (2011) admitted "the possibility that some 'helping' behaviours, usually assumed to represent altrustic co-operation, may represent mutualistic forms of co-operation and even selfishness" (p527).

Co-operative breeding can also include general group benefits like communal defence and predator dilution effects (ie: risk of predation for individual animal is reduced), and thermoregulation (ie: keeping warm together) as well as specific ones like baby-sitting and nursing.

The benefits of co-operative breeding can be seen in relation to solitary breeding where both types exist in the same species, as in warthogs (Phacochoerus africanus) (figure 3.1) (White and Cameron 2011). In fact, these animals show three strategies based on observations of female warthogs in a South African Game Reserve:

- Solitary breeding - one female and offspring (n = 15).
- Co-operative breeding - one female and offspring and yearlings as helpers (n = 9).
- Communal breeding - multiple adult females and offspring (and yearling helpers) (n =23).

(Source: Quartl)

Figure 3.1 - Common warthog.

Adult females appeared to baby-sit more often than yearlings suggesting that communal breeding was the most advantageous reproductive strategy. Baby-sitting behaviour was reciprocated by the females and this explained its existence among genetically unrelated individuals (White and Cameron 2011).

Offspring raised by parents and helpers benefit in ways beyond the obvious survival. For example, meerkats (Suricata suricatta) (figure 3.2) gained extra food from helpers which led to an earlier age of first reproduction, and subsequently a more dominant position in the group (Russell et al 2007).

(Source: Quartl)

Figure 3.2 - Meerkat.

On the negative side, helpers may become competitors for juveniles for access to mates. For example, less male juvenile Alpine marmots (Marmota marmota) survived where male helpers were present compared to parents only upbringing (Allaine and Theuriau 2004).

One question is whether offspring raised with helpers benefit in later life. In the case of birds, after leaving the nest (post-fledging).

Covas et al (2011) attempted to answer this question using the capture-mark-recpature (CMR) method with the sociable weaver bird (Philetairus socius) (figure 3.3) at Benfontein Game Farm in Northern Cape Province, Republic of South Africa (figure 3.4). With the CMR method the birds are initially caught and marked with coloured bands, and then recaptured at a later date to see who has survived. This happened between 1999 and 2005.

Sixty-two birds raised by pairs (parents) were compared to 51 raised by groups (parents with 1-3 helpers). First-year survival was found to be 7% lower among fledglings raised by groups, but there was no difference in the longer term. The finding that birds raised by parents only were more likely to survive was a surprise.

Covas et al (2011) suggested a number of explanations. One was that parents with helpers use the opportunity to aid their own survival, and so the parents' feeding rate of the offspring is less than for parents alone. In other words, the majority of the feeding was the responsibility of the helpers who may not be efficient.

On the other hand, the findings were based on the recapture of birds. Birds raised by groups may have left the study area, and this accounts for the results.

(Source: Anagoria)

Figure 3.3 - Sociable weaver.

(Drawn with MapCreator2)

Figure 3.4 - Approximate site of Benfontein Game Farm,
South Africa.

3.2. APPENDIX 3A - "PAY-TO-STAY"

There is a question of what do the genetically
unrelated helpers gain for their co-operative behaviour.
One answer is called "pay-to-stay". Helping is the
"payment" for being tolerated in the territory of the
dominant animal.

Non-kin helpers are common among cichlid fish (eg:
Neolamprologus pilcher) in Lake Tanganyika, Central
Africa. A dominant pair with have 5-8 adult helpers and
additional offspring in their territory (Bruintjes and
Taborsky 2008).

Bruintjes and Taborsky (2008) made the following
predictions about cichlid behaviour from the "pay-to-
stay" hypothesis:

i) In high perceived population density situations,
helpers will "pay more" (eg: risky defence behaviour
rather than territory maintenance behaviours like digging
sand away from the breeding shelter).

ii) Large helpers will "pay more" (ie: more helping behaviours) than small ones because the larger fish are a greater threat to the territory's owners in terms of territorial take-over.

iii) Male helpers will "pay more" than female helpers because males are a greater threat to the dominant breeding pair.

These predictions were tested in large tanks at the University of Bern, Switzerland. In the experiments, the perceived population density was varied along with the size and sex of helpers (figure 3.5). Two of the three predictions were supported by the findings:

- Helpers performed significantly more defence behaviours in high perceived population density environments.
- Large helpers carried out significantly more defence and digging behaviours than small helpers (table 3.1).
- Helper sex had no effect on amount of defence behaviour.

Area for fish to create population density

Study area

Breeding male

Breeding female

Large helper
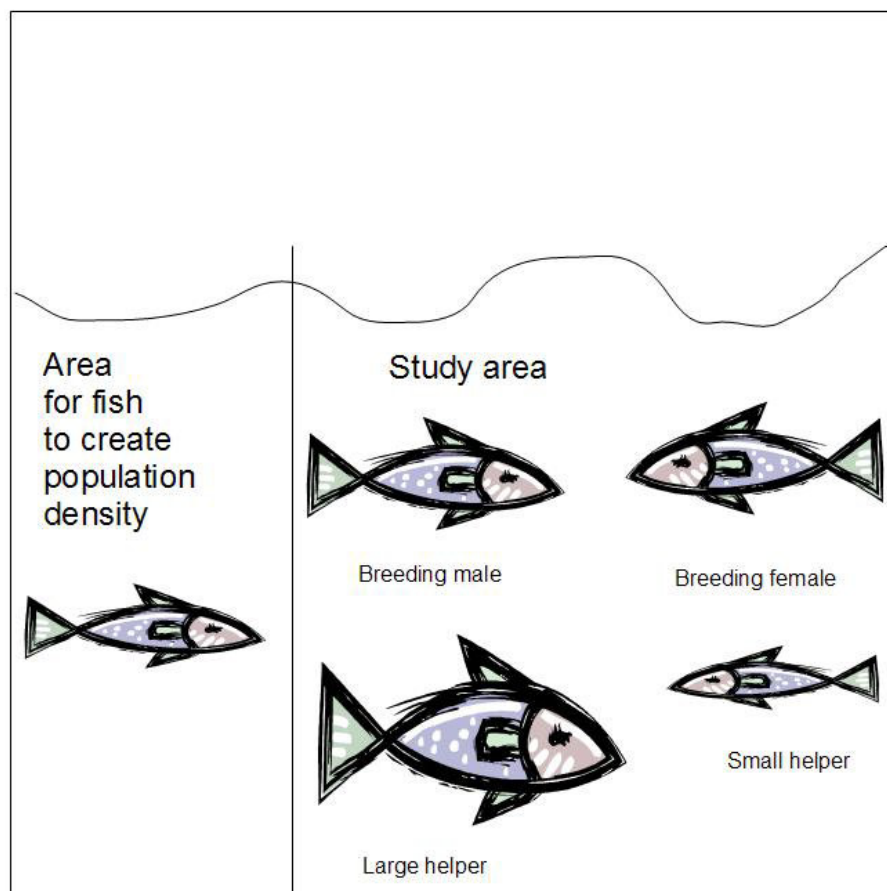
Small helper

(Based on Bruintjes and Taborsky 2008 figure 1 p1845)

Figure 3.5 - Design of tank used in experiments.

	LARGE HELPER	SMALL HELPER
HIGH PERCEIVED DENSITY	19 (a)	4 (c)
LOW PERCEIVED DENSITY	14 (b)	<1 (d)

(a > b; c > d; a/b > c/d; all significant p<0.05)

(Source: Bruintjes and Taborsky 2008 figure 2 p1846)

Table 3.1 - Approximate median number of defence behaviours per ten-minute observation period.

3.3. REFERENCES

Allaine, D & Theuriau, F (2004) Is there an optimal number of helpers in Alpine marmot family groups? Behavioural Ecology 15, 916-924

Bruintjes, R & Taborsky, M (2008) Helpers in a co-operative breeder pay a high price to stay: Effects of density, helper size and sex Animal Behaviour 75, 1843-1850

Covas, R et al (2011) The effect of helpers on the post-fledging period in a co-operative breeding bird, the sociable weaver Animal Behaviour 81, 121-126

Russell, A.F et al (2007) Helpers increase the reproductive potential of offspring co-operative meerkats Proceedings of the Royal Society B 274, 513-520

Stiver, K.A et al (2005) Relatedness and helping in fish: Examining the theoretical predictions Proceedings of the Royal Society B 272, 1593-1599

White, A.M & Cameron, E.Z (2011) Evidence of helping behaviour in a free-ranging population of communally breeding warthogs Journal of Ethology 29, 419-426

Wong, M & Balshine, S (2011) The evolution of co-operative breeding in the African cichlid fish, Neolamprologus pulcher Biological Reviews 86, 511-530

Woolfenden, G.E (1975) Florida scrub jay helpers at the nest Auk 92, 1-15

Zahavi, A (1995) Altruism as a handicap - the limitations of kin selection and reciprocity Journal of Avian Biology 26, 1-3

4. DEFENDING TERRITORY

4.1. EXAMPLES OF BIRDS

In some species males establish, maintain, and defend territories for breeding. In such species there will also be non-territorial males who wait for territorial vacancies (ie: resident dies or leaves) or they try to overthrow residents. These "floaters" usually have less reproductive success (ie: less offspring) than residents [14].

For residents, two important factors are timing of territory establishment (in relation to arrival of females to breed), and site fidelity (whether to remain in or return to the same site in consecutive breeding seasons). Early establishment allows access to the best sites, and site fidelity leads to familiarity with resources and risks, and both these factors are associated with greater reproductive success usually (Hughes and Hyman 2011) (table 4.1).

EARLY ESTABLISHMENT OF TERRITORY:	SITE FIDELITY:
 • Access to higher quality territory. • Opportunity to develop familiarity with resources and predator risks. • But more energy expended on longer period of territorial defence.	 • Familiarity with habitat. • Establish relationships with neighbours, and ability to distinguish invaders and nature of threat (eg: shared songs learned among neighbours; Beecher et al 1994).
LATE ESTABLISHMENT OF TERRITORY: • Easier to invade high quality territory when resident involved in parental care. • But miss opportunity to engage in extra-pair copulations.	MOVING SITES: • Loss of relationships with neighbours. • May be able to find better quality territory. • Some males may be forced to move by losing to invaders. These males show they have low resource holding potential.

Table 4.1 - Costs and benefits of territory establishment and site fidelity.

---

[14] Though this is not always the case (eg: Raihani et al 2008) (appendix 4A).

Hughes and Hyman (2011) investigated the territorial behaviour of male song sparrows (Melospiza melodia) in north-west Pennsylvania, USA, over a nine-year period. These birds migrate a short distance within the USA, and return to establish territories in early March - mid-April for the females' arrival in mid-late April. "Late establishers" were defined as males arriving after hatching had begun (early May). The birds were also categorised as non-movers or movers based on whether they returned to the same territory on consecutive breeding seasons. This information was obtained by banding the birds with a unique combination of coloured bands on their legs. The sample was 88 males, of which 48 were early establishers/non-movers, 18 early establishers/movers, 13 late establishers/non-movers, and 9 were late establishers/movers.

Early establishing males had more successful nests (ie: young who fledged) than late establishers, but late establishing males who moved territory were more successful than early establishing movers. Overall, late establishers did better to move territory the next year, while there was no difference for early establishers between moving or not moving in terms of successful nests. The authors noted: "While early territory establishment and high site fidelity are clearly the norm, behaviours such as late territory establishment and territory relocation cannot be dismissed as anomalous or indicative of low-quality individuals" (Hughes and Hyman 2011 p989).

Piper et al (2011) reported that "floaters" among the common loon (Gavia immer) (figure 4.1) tended to target the territory of successful breeders because territory that produced chicks in one year was also likely to do so the next year (eg: due to few egg predators). This benefit of a territory would explain the energy expended by floaters attempting to take-over a territory (eg: one-third of male take-overs result in death for a combatant).

But such fierce battles over territory are more common among species that have only one opportunity to mate (ie: short-lived species like fig wasps or spiders; Piper et al 2011). But loons live for up to 20 years, so why would they risk so much in territorial fights?

One possible answer is that a territory is re-used over many years, and so defending a successful site increases reproductive success beyond the single breeding season. This is the "familiarity" hypothesis (Piper et al 2011).

Males with past breeding success in a territory are 41% more likely to produce chicks successfully subsequently in that territory (based on observations of lakes in Oneida County, Wisconsin, USA by Piper et al 2011).

Resident males have good reason to fight to the death to defend their territory (more so than intruders), and the majority of dead birds found were territory owners (Piper et al 2011). But the improved reproductive success of guarding a territory is not enough to risk death. Displaced males could recover their lost reproductive success within 3-5 years.

An alternative explanation is the "desperado" hypothesis (Piper et al 2011). It is the older male territory owners who fight to the death because they do not have the option of moving and regaining reproductive success in the future.

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

Figure 4.1 - Common loon.

4.2. APPENDIX 4A - SWITCHERS

Among a type of insects, odonates like the American rubyspot damselfly (Hetaerina americana) (figure 4.2), territorial males usually have greater reproductive success than non-territorial males, and being successful

territorially is linked to fat reserves on the thorax as
territorial defence involves high energy expenditure
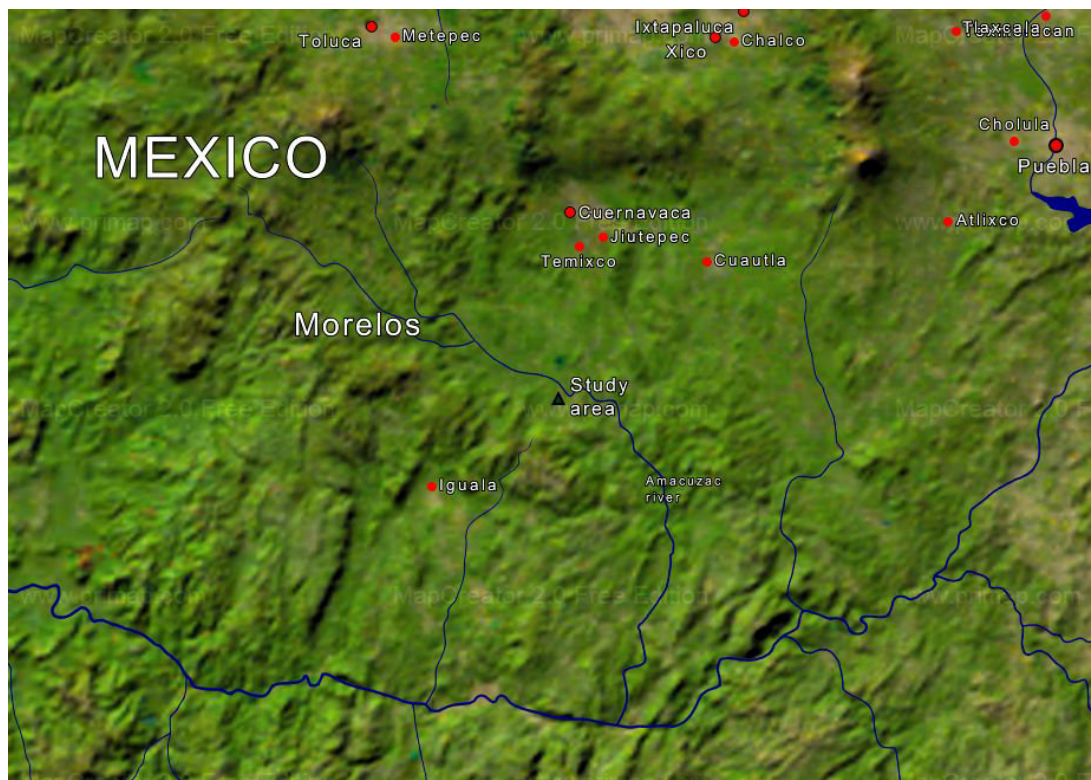(Raihani et al 2008).

(Source: Eugene Zelenko)

Figure 4.2 - Male American rubyspot damselfly.

      So males with large fat reserves will be territorial
and males with small reserves will be non-territorial.
But Raihani et al (2008) found, in their fieldwork in
southern Mexico on the shores of the Amacuzac river
(figure 4.3), that some males switched, showing both
territorial and non-territorial behaviour. This involved
defending the same area (eg: 10 metres of riverbank) for
a certain period of time (eg: one day), then becoming
non-territorial for a day, for example, and finally
returning the next day to defend the original territory.
These insects had intermediate fat reserves.

Of 148 males marked and observed by the researchers, 74 were territorial, 53 non-territorial, and 21 switchers. There was no difference in the number of copulations between the three groups of males.

(Drawn with MapCreator2)

Figure 4.3 - Approximate area of Raihana et al (2008) study in southern Mexico.

4.3. REFERENCES

Beecher, M.D et al (1994) Correlation of song learning and territory establishment strategies in the song sparrow Proceedings of the National Academy of Sciences, USA 91, 1450-1454

Hughes, M & Hyman, J (2011) Should I stay or should I go now: Late establishment and low site fidelity as alternative territorial behaviours Journal of Ethology 117, 979-991

Piper, W et al (2011) Marking loons, making progress American Scientist 99, May-June, 220-227

Raihani, G et al (2008) Male mating tactics in the American rubyspot damselfly: Territoriality, non-territoriality and switching behaviour Animal Behaviour 75, 1851-1860

5. RECOGNISING INDIVIDUAL CALLS

5.1. CALLS OF INDIVIDUALS

In certain mammal species, recognition of an individual's call is possible [15]. For example, where vocal effort (eg: loudness, or length of calling) is a male sign of "good quality" (eg: red deer; Reby et al 2001; appendix 5B), then females need to recognise the individual with the best calling. In other situations, parents need to recognise their individual offspring (eg: fur seal pups; Charrier et al 2003; appendix 5C) or closely related kin from strangers (eg: rhesus monkeys; Rendall et al 1996), and individual alarm callers (eg: Richardson's ground squirrels; Hare 1998; appendix 5D). The key in all these cases is that the individual's vocalisations must be distinctive and/or unique, and that the hearer can distinguish one caller from another. It is assumed that if one of these evolved then so did the other.

This can be tested using the habituation-discrimination paradigm. One call is played a number of times until the listener is habituated to it, then a different call is played. If the listener can discriminate different calls, they will show interest when hearing the novel call, whereas there will be no reaction if individual callers are not distinct.

Charlton et al (2009) used this method with male giant panda (Ailuropoda melanoleuca) bleats played to females in China. The researchers played the captive females eight bleats in a row with 20-second gaps between them, of which the first six were the same male (habituation phase), the seventh was a different male, and the eight the original male again. Discrimination by the female was measured by turning the head towards the sound.

The females looked significantly more often towards the sound after the seventh call (new male) as compared to the 6th and 8th calls (original male). This suggested that the females could distinguish between individual male callers.

---

[15] Recognition of individual animals is also done visually via the face (appendix 5A).

5.2. APPENDIX 5A - FACE RECOGNITION

The recognition of individual faces is common among primates, and the brain has evolved specialised "modules" for doing so (Chittka and Dyer 2012). Recent research has expanded this ability to include an insect, the paper wasp (Polistes fuscatus) (figure 5.1) (Sheehan and Tibbetts 2011).

In this species, several queens form a new nest, then they battle for supremacy. After duels, individuals subsequently recognise the winner and loser by their distinct facial markings, and there are no more fights (Chittka and Dyer 2012).

(Source: Bruce.J.Martin; http://www.cirrusimage.com/Bees_wasp_Polistes_fuscatus.htm)

Figure 5.1 - Polistes fuscatus.

Sheehan and Tibbetts (2011) tested the wasps' facial recognition ability by offering two arms of a maze, each marked with an image. The correct choice allowed safety and the wrong choice produced an electric shock. The image pairs were normal or manipulative wasp faces, with

simple geometric patterns or prey (caterpillars) as controls. Polistes metricus are a species of wasp where individual queens start a nest, and they do not need face recognition skills. They were used as a comparison group.

The individual Polistes fuscatus wasps were able to recognise normal wasp faces, but not scrambled faces nor normal faces without antennae (tables 5.1 and 5.2).

TWO IMAGES	NUMBER CORRECT
Polistes fuscatus own species' face	6.5
Patterns	5
Caterpillars	4.5
Antennae-less faces	5
Polistes metricus own species' face	5

(5 = chance)

(Source of data: Sheehan and Tibbetts 2011 figure 2 p1273)

Table 5.1 - Mean correct choice of two images out of 10.

IMAGE	Polistes fuscatus	Polistes metricus
Own species face	>70	<50
Pattern	65	60
Caterpillars	50	55
Antennae-less face	60	-
Rearranged face	60	-

(50% = chance)

(Source of data: Sheehan and Tibbetts 2011 figure 3 p1274)

Table 5.2 - Mean percentage correct choices of image versus non-face/manipulated face.

5.3. APPENDIX 5B - REBY ET AL (2001)

During the 4-5 weeks of reproduction each year, red deer (Cervus elaphus) stags roar loudly to show the quality of their genes to females which are herded in harems, and towards other males. In the former case, females choose the best male through familiarity resulting from hearing the call over time (and other cues like visual and olfactory). This is called the "mate-investment hypothesis" and requires that females can distinguish the different male callers.

Reby et al (2001) performed a playback experiment with red deer (24 hinds) at an experimental farm in

France. Roars were recorded from four stags. They were played back using the habituation-discrimination paradigm: ten roars from stag A, 11th roar from stag B, and the 12th from stag A again. Attention was measured as orienting ears towards the speakers by a hind (length of time in seconds, and speed of behaviour starting in seconds).

The hinds responded significantly longer to roar 11 (stag B) than to roar 10 or 12 (stag A) (mean 12 vs 4 seconds; p = 0.008), and started significantly quicker (figure 5.2). This suggested the recognition of individual callers.
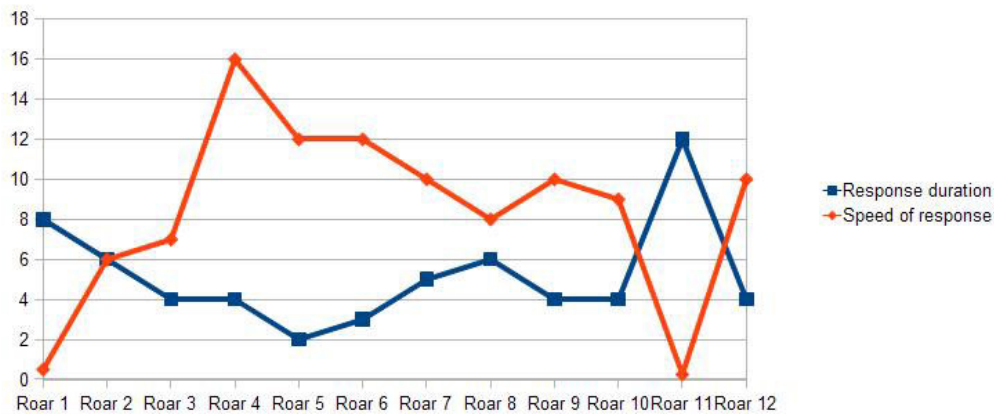
(Data from Reby et al 2001 figure 1 p957)

Figure 5.2 - Response duration and speed of response.

5.4. APPENDIX 5C - RECOGNITION OF INDIVIDUAL KIN

For parents, recognition of individual offspring stops misdirection of parental care, while offspring need to recognise their parents in order to receive feeding, particularly in a colony. Recognition of the individual caller on both sides is key here.

However, there are differences between parents and offspring. For example, Insley (2001) found that, in playback experiments with northern fur seals, mothers responded only to their pup's calls, while pups would sometimes respond to another female's calls. "From an evolutionary point of view, parent-offspring conflict theory emphasises that the selection pressures acting on mothers and pups are different (Trivers 1974).

Recognition is crucial to the pups' survival, whereas an error in recognition represents a smaller cost for adult females; therefore, for pups selection may favour probing and deception, and necessitates a more liberal acceptance criterion..." (Charrier et al 2003 pp543-544).

Sub-Antarctic fur seal (Arctocephalus tropicalis) mothers leave their pups (figure 5.3) on the beaches in colonies while hunting for food in the sea. Returning to the beach the female's calls cause the pup to call, look around, and finally approach the mother. Reunion using this system occurs quickly. Less than seven minutes in a study by Charrier et al (2003) of a colony of over 500 mother-pup pairs on Amsterdam Island (French Southern and Antarctic Lands) in the Indian Ocean (figure 5.4).

(Source: Nicolas Servera; otarie_sans@yahoo.fr)
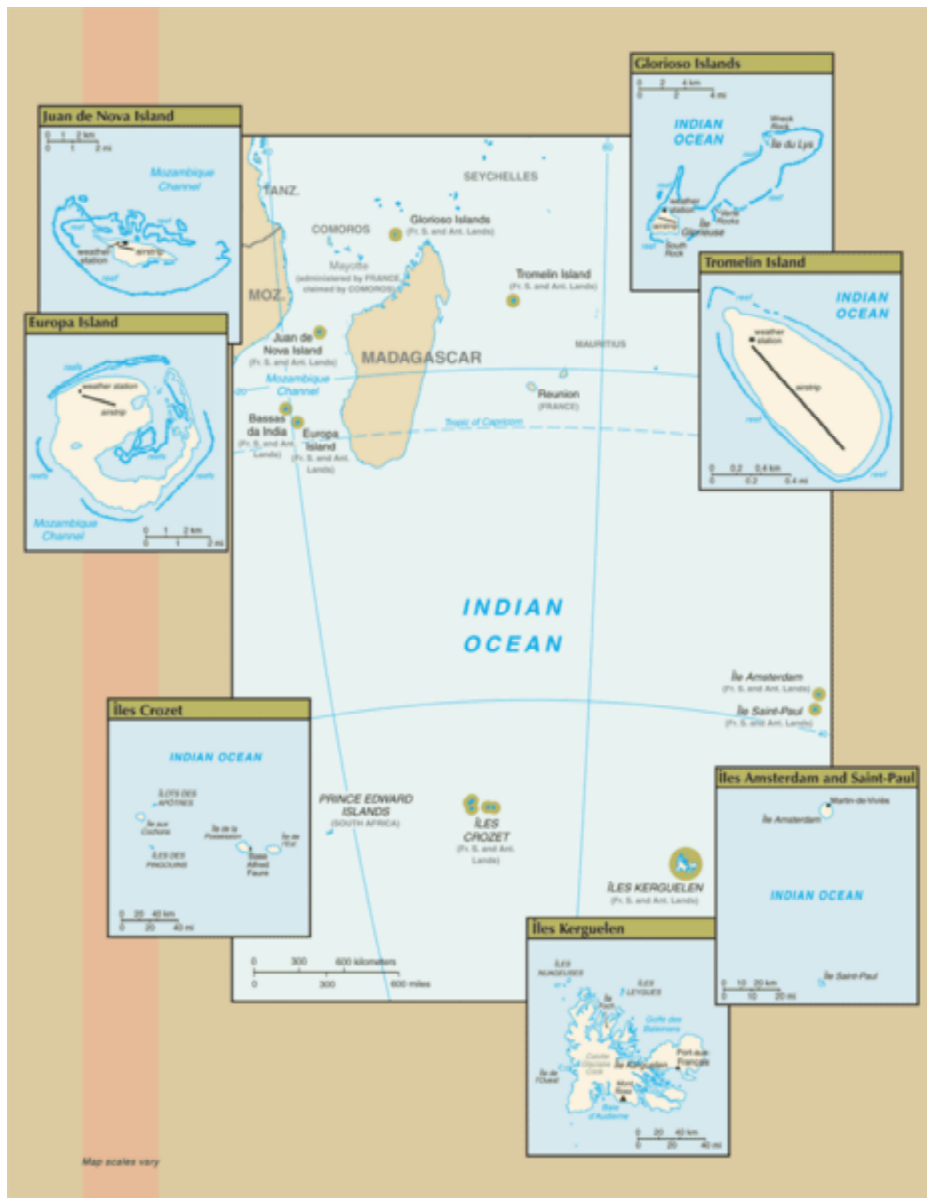
Figure 5.3 - Arctocephalus tropicalis pup.

Charrier et al (2003) altered the calls of mothers and pups to isolate the key acoustic components in recognition. For mothers, the main criterion was frequency modulation (which meant they could recognise the pup's call played backwards) [16]. Pups used frequency

---

[16] The call varies in frequency (kHz) ie: goes up and down.

(Source: Central Intelligence Agency's World Factbook; in public domain)

Figure 5.4 - Position of Amsterdam Island.

modulation, and the harmonics of the mother's calls [17]
(and half of the pups could recognise their mother's
calls played backwards).

Aubin and Jouventin (2002) reported individual
recognition based on amplitude and frequency modulations
of calls among six species of penguin - little penguins
(Eudyptula minor) in Australia, Adelie penguins
(Pygoscelis adeliae) and emperor penguins (Aptenodytes
forsteri) in Antarctica, and king, macaroni and gentoo

_____

[17] The "melody" or tone of the call.

penguins (Aptenodytes patagonicus, Eudyptes chrysolophus, Pygoscelis papua) in sub-Antarctic islands.

Frommolt et al (2003) found that Arctic foxes (Alopex lagopus) on Mednyi Island in the north Pacific [18]could distinguish between the barks of their social group members and other social groups.

Calls were played of an own group member or an "alien" (neighbouring group member or stranger). The calls of own group members from a loud speaker hidden in the undergrowth produced greetings (fox whimpered), while the common response to "aliens" was to bark (with scent marking - territorial behaviour).

5.5. APPENDIX 5D - HARE (1998)

Identifying an individual caller helps in relation to alarm calls if it is a neighbour or non-neighbour giving the warning, and the imminent risk of danger. An alarm call from a neighbour requires quicker action than from a distant non-neighbour.

Hare (1998) found the ability to discriminate individual alarm callers among juvenile Richardson's ground squirrels (Spermophilus richardsonii) near Manitoba, Canada. A series of five alarm calls for an avian predator were played. In the experimental condition, four calls were from one individual and the fifth from another individual, while all five were from the same individual in the control condition. Sometimes a neighbour was used, and sometimes a non-neighbour. The vigilance behaviour of the listener was measured.

The fifth call from a different individual produced a significant increase in vigilance behaviour (standing on the hind legs with the back erect) (over twice as long) from the previous call, and compared to the 5th call in the control condition.

5.6. REFERENCES

Aubin, T & Jouventin, P (2002) How to vocally identify kin in a crowd: The penguin model Advances in the Study of Behaviour 31, 243-277

Charlton, B.D et al (2009) Vocal discrimination of potential mates by female giant pandas (Ailuropoda melanoleuca) Biology Letters 5, 5, 597-599

Charrier, I et al (2003) Vocal signature recognition of mothers by fur seal pups Animal Behaviour 65, 543-550

Chittka, L & Dyer, A (2012) Your face looks familiar Nature 481, 154-155

Frommolt, K-H et al (2003) Barking foxes, Alopex lagopus: Field

---

[18] One of the Commander Islands (or Komandorski Islands), part of the Russian Federation.

experiments in individual recognition in a territorial mammal <u>Animal Behaviour</u> 65, 509-518

Hare, J.F (1998) Juvenile Richardson's ground squirrels, Spermophilus richardsonii, discriminate among individual alarm callers <u>Animal Behaviour</u> 55, 451-460

Insley, S.J (2001) Mother-offspring vocal recognition in the northern fur seal <u>Nature</u> 406, 404-405

Reby, D et al (2001) Red deer (Cervus elaphus) hinds discriminate between the roars of their current harem-holder stag and those of neighbouring stags <u>Ethology</u> 107, 951-959

Rendall, D et al (1996) Vocal recognition of individuals and kin in free-ranging rhesus monkeys <u>Animal Behaviour</u> 51, 1007-1015

Sheehan, M.J & Tibbetts, E (2011) Specialised face learning is associated with individual recognition in paper wasps <u>Science</u> 334, 1272-1275

Trivers, R.L (1974) Parent-offspring conflict <u>American Zoologist</u> 14, 249-264

6. SLEEP IN FISH AND INSECTS

6.1. INTRODUCTION

It is generally assumed all animals sleep and that sleep deprivation is detrimental. "Together, these two assumptions suggest that a universal, vital function is accomplished in sleep" (Siegel 2008 p208). Most interest and research has been in relation to mammals with little time (maybe for practical reasons) on sleep in fishes. Siegel (2008) observed that less than ten species had been studied in the laboratory (out of the total of 30 000 plus species of fish).

One issue is how to define sleep. Sleep in fish and insects is defined by behavioural criteria because of the problems of getting electrographic recordings of brain activity. Definitions include criteria like quiescence (reduced activity and movement [19]) and increased arousal threshold (to electrical stimulation, for example).

6.2. FISHES

Fish show periods of rest and activity in 24 hours, but the question is whether the rest is sleep. The answer is maybe. In the limited number of EEG studies of fish the results are contradictory - some show changes in brain waves during behavioural sleep (eg: catfish; Ictalurus nebulobus) and others do not (eg: tench; Tinca tinca) (Tobler and Borbely 1985).

While two types of rest have been observed in guppie (Tilapia mossambica) (Tobler and Borbely 1985).

Here are some examples of species that have been studied in some detail.

1. Zebrafish (Danio rerio)

Yokogawa et al (2007) described a "sleep-like state" with immobility and increased arousal threshold. Long periods of light stopped this behaviour without a subsequent rebound, but there was rebound after deprivation by electrical stimulation.

---

[19] Immobility in a stereotypical posture or a species specific posture (Klein and Seeley 2011).

Cirelli and Tononi (2008) reported changing brain electrical activity during the "sleep-like state" in this species.

2. Perch (Cichlosoma nigrofasciatum)

Tobler and Borbely (1985) performed experiments with perch which produced rest deprivation through continuous light. After the deprivation, the fish showed more rest and less activity (ceasing swimming and remaining motionless). But this rest was not necessarily "sleep" (Siegel 2008). Also no measurement of arousal threshold was made (Cirelli and Tononi 2008).

3. Coral reef fish

Cirelli and Tononi (2008) noted two types of sleep among these species - immobile and "sleep swimming" (continuous night time activity).
Goldshmid et al (2004) reported "sleep-swimming" by three species (Dascyllus marginatus, Dascyllus aruanus, Chromis viridis) in the Red Sea. As they moved around the stroke frequency of the dorsal, pectoral and caudal fins was greater than when awake. The researchers viewed it as "equivalent to sleep" (an intermediate state between full sleep and apparent wakefulness) with no response to stimulation by light or the presence of predators.
Certain species have a smaller response to electrical stimulation during inactive periods (Siegel 2008).
Cirelli and Tononi (2008) reported reduced sleep onset latency after deprivation, but no increase in total sleep time among certain of these species.

4. Tuvira (Gymnotus carapo L)

The tuvira discharges a low voltage electrical pulse into the water as a means to scan the area and as communication. Stopa and Hoshino (1999) measured this discharge, in twenty individuals captured in the Parano River, Brazil, to see if it changed during prolonged immobility and reduced fin movement (behaviourally defined sleep). The discharges changed during sleep but were not absent. The researchers felt that this was enough evidence that this fish species does sleep.

6.3. INSECTS

Of over 700 000 species of insect (Siegel 2008), three have been studied in some detail (cockroaches,

fruit flies and bees). "Clearly the anatomical and some of the neurochemical properties of sleep cannot exist in insects, because of the differences in the structure of the nervous systems" (Siegel 2008 p209).

1. Cockroach

Tobler (1983) found that a three-hour rest deprivation by forced activity in one species of cockroach (Leucophen maderae) produced greater immobility in the first hour after recovery.

Tobler and Neuner-Jehle (1992) created a six-hour rest deprivation by handling in the cockroach (Blaberus giganteus), and this produced subsequent rest with the lowest arousal level (ie: "deep sleep").

2. Honey bee

Honey bees (Apis mellifera) "experience a process that is similar to mammalian sleep" (Sauer et al 2004). This is based on high arousal thresholds and antennal immobility.

Sauer et al (2004) deprived bees of sleep for 12 hours by placing individuals in cylinders on a tilting device which produced enforced activity. The bees compensated for this deprivation with increases in antennal immobility the next night (twice as much as controls) and a "deeper" sleep (based on arousal threshold). Antennal immobility was measured by close-up video-recording, and categorisation of behaviour as immobility, small movement, antennal movement, or antennal activity.

Klein and Seeley (2011) showed that honeybees can adapt their "sleep" period depending on when food is available. One small colony was trained to forage in the morning, and another colony in the afternoon. The former group slept more in the afternoon, and the latter group in the morning. The researchers saw this adaptation of sleep as "analogous to the way that humans employed in some organisations must shift their sleep schedules to accommodate shifts in their work schedules" (Klein and Seeley 2011 p82).

3. Fruit fly

Shaw et al (2000) reported the study of flies (Drosophila melanogaster) using an ultrasound activity monitoring system that detects the movement of head, wings and limbs. From this it was found that the flies were inactive during dark periods in 12-hour light/12-hour darkness regime. Hendricks et al (2000) recorded

complete immobility with only respiratory abdominal pumping movements of up to 26 minutes. In total, "sleep" lasted for an average of approximately 2.5 hours (157 minutes).

Shaw et al (2000) determined the arousal threshold by vibratory stimuli. When awake the flies responded to intensities of 0.05g and 0.1g, but after five minutes of rest they reacted to these intensities less than 20% of the time. Thus an increased arousal threshold associated with rest. Hendricks et al (2000) used tapping the container to gauge arousal. Resting flies needed significantly stronger tapping to arouse them.

Flies deprived of rest for 12 hours by gentle tapping showed a subsequent increase in rest in the next 12 hours. Shaw et al (2000) also reported that the amount of rest decreased with age.

Shaw et al (2000) concluded that "behavioural, pharmacological, molecular, and genetic investigations indicate that Drosophila rest shares many critical features with mammalian sleep" (p1836). Hendricks et al (2000) preferred to call the rest a "sleep-like state".

6.4. CONCLUSIONS

Siegel (2008) concluded in relation to all animals:

It might well be more accurate to view sleep as a behaviour whose presence, quality, intensity and functions vary between species and across the lifespan. Different animals have used sleep to maximise energy savings by reducing body and brain energy consumption, increasing survival by seeking out a safe sleeping site, releasing hormones and conducting a variety of recuperative processes. Some species appear to be able to accomplish these processes during the waking state. This view contrasts with the idea that sleep is a universal state with the same underlying vital function in all species (p212).

6.5. REFERENCES

Cirelli, C & Tononi, G (2008) Is sleep essential?" PLoS Biology 6, 8, e216

Goldshmid, R et al (2004) Aeration of corals by sleep-swimming fish Limnology and Oceanography 49, 5, 1832-1839

Hendricks, J.C et al (2000) Rest in Drosophila is a sleep-like state Neuron 25, 129-136

Klein, B.A & Seeley, T.D (2011) Work or sleep? Honeybee foragers opportunistically nap during the day when forage is not available Animal Behaviour 82, 77-83

Sauer, S et al (2004) Sleep deprivation in honey bees Journal of Sleep Research 13, 145-152

Shaw, P.J et al (2000) Correlates of sleep and waking in Drosophila melanogaster <u>Science</u> 287, 1834-1837

Siegel, J.M (2008) Do all animals sleep? <u>Trends in Neuroscience</u> 31, 4, 208-213

Stopa, R.M & Hoshino, K (1999) Electrolocation-communication discharges of the fish Gymnotus carapo L (Gymnotidae: Gymnotiformes) during behavioural sleep <u>Brazilian Journal of Medical and Biological Research</u> 32, 1123-1228

Tobler, I (1983) Effect of forced locomotion on the rest-activity cycle of the cockroach <u>Behaviour and Brain Research</u> 8, 551-560

Tobler, I & Borbely, A (1985) Effect of rest deprivation on motor activity of fish <u>Journal of Comparative Physiology A</u> 157, 817-822

Tobler, I & Neuner-Jehle, M (1992) 24-hour variation of vigilance in the cockroach Blaberus giganteus <u>Journal of Sleep Research</u> 1, 231-239

Yokogawa, T et al (2007) Characterisation of sleep in zebrafish and insomnia in hypocretin receptor mutants <u>PLoS Biology</u> 5, 10, e277