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Animal Topics

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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. MOVEMENTS AND NAVIGATION

1.1. INTRODUCTION

Among running animals, "the largest are not the fastest", and Hirt et al (2017) explained this fact with "a maximum-speed model based on the concept that animals are limited in their time for maximum acceleration because of restrictions on the quickly available energy. Consequently, acceleration time becomes the critical factor determining the maximum speed of animals" (p1116).

1.2. DISPERSAL

Organisms move to satisfy basic needs ("foraging" movements), to relocate to a novel area (dispersal), and to escape temporary environmental changes (migration) (Cote et al 2017) (table 1.1).

- The Monarch butterfly (Danaus plexipus) migrates vast distances from North America to Mexico to overwinter (up to 4000 km), and then northwards to the southern USA to deposit their eggs on milkweed plants. Migrants have increased longevity, abdominal fat stores, and cold tolerance.

- Navigation is by time-compensated sun compass through the eye, while the brain integrates circadian information. "In migrating monarchs, the horizontal position of the sun (solar azimuth) and the derived polarised skylight pattern provide directional cues for the sun compass... The solar azimuth is likely sensed by the main retina, whereas polarised light is sensed by the specialised dorsal rim area, a small region of the compound eye anatomically specialised for sensing the angle of plane-polarised skylight" (Zhan et al 2011 p1175).

- Guerra and Reppert (2013) reported that coldness triggers the northward flight direction. The researchers manipulated the light/dark periods and the temperature in their experiments. Guerra and Reppert (2013) concluded that their study "clearly show that individual monarch butterflies use a time-compensated sun compass to direct their migration both southward and northward.

> Moreover, the sun compass mechanism is modulated primarily by cold exposure during overwintering to flip the butterflies' orientation direction from south (in the fall) to north (in the spring). The data show, unexpectedly, that the thermal microenvironment at the overwintering site is critical for successful completion of the migration cycle. Without coldness, eastern North American migrants cannot reverse their flight direction, and the migration cannot progress" (p422).

Table 1.1 - Monarch butterfly.

Dispersal is seen as a solitary enterprise [1], whereas migration is a collective behaviour. "Both dispersal and migration involve three steps: individuals leave their current habitat patch (here defined as an area of sufficient size and resources for an individual to be able to maintain itself for a given period of time: natal or breeding range for dispersal; breeding or wintering range for migration), travel across the landscape (ie: transience), and finally settle in a novel habitat patch (ie: settlement: breeding range for dispersal; breeding or wintering range for migration)" (Cote et al 2017 p1277).

Dispersal from the place of birth (natal habitat) or breeding area avoids competition with kin and risk of inbreeding, and competition over scarce resources with non-kin and other species (Cote et al 2017).

One theory is that dispersal is a precursor in a species to the evolution of migration (eg: birds; Salewski and Bruderer 2007). Individuals disperse to areas that are unsuitable part of the year, and so move back to their point of origin, and repeat this behaviour the next year.

Collective movements develop when individuals learn about the suitability of a habitat from others, say. This idea of collective decision-making is the "many-wrongs principle" (Simons 2004), which states that "if each individual makes their own, error-prone, assessment, but then tends to align with the direction of motion of others, environmental noise can be dampened due to multiple sampling by individuals within a group" (Cote et al 2017 p1286).

In terms of collective decision-making, there are four types of models based on the amount of information (Cote et al 2017):

a) Quorums - most individuals have the information (eg: where new food patch is) and the decision emerges

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[1] Exceptions include green iguana hatchlings leaving their place of birth in groups (known as "budding dispersal") to reduce the individual predation risk, while the bird, the Arabian babbler, can disperse individually or in groups (Cote et al 2017).

from them (eg: to move to new food patch).

b) Leadership - certain individuals have the information and others benefit from following what these individuals decide to do.

c) Independence-interdependence - the pooling of information from multiple individuals.

d) Social parasitism - individuals exploit those who have information.

1.3. NOMADISM

The distinction between dispersal and migration can be unclear in nomadic species, who are "not strongly faithful to any particular range or area" (Cote et al 2017 p1285). Should movement in these animals be "considered as a form of non-seasonal and undirected migration or a form of recurring breeding dispersal" (Cote et al 2017 p1285)?

The pectoral sandpiper (Calidris melanotos) (figure 1.1) is a polygynous species with the males competing for access to females without providing resources (other than sperm) or offspring care (appendix 1A). Where the females are based, local competition by males for mating opportunities is intense, and only a few males succeed in breeding (Kempenaers and Valcu 2017) [2].

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

Figure 1.1 - Pectoral sandpiper.

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[2] Competition via secondary sexual ornaments used in displays (eg: fully developed throat sac).

Kempenaers and Valcu (2017) studied the movements of males around breeding sites in Barrow (Alaska) with satellite-based telemetry in the 2012 and 2014 breeding seasons.

The average distance travelled around Alaska, and the Canadian and Russian Arctic was 3000 km, which included up to 24 different potential breeding sites [3]. Males stayed at a particular breeding site for 1-2 days, and movements were driven by the local availability of fertile females.

This behaviour was described as "nomadism", which describes individuals that "move at any time and in any direction between successive breeding sites, and over shorter or longer distances" (Newton 2010 quoted in Kempenaers and Valcu 2017). Most migratory birds reside in a single area for the breeding season (Kempenaers and Valcu 2017).

Males wander through different breeding sites and "opportunistically display and compete at different sites within a single breeding season" (Kempenaers and Valcu 2017 p530) (figure 1.2).

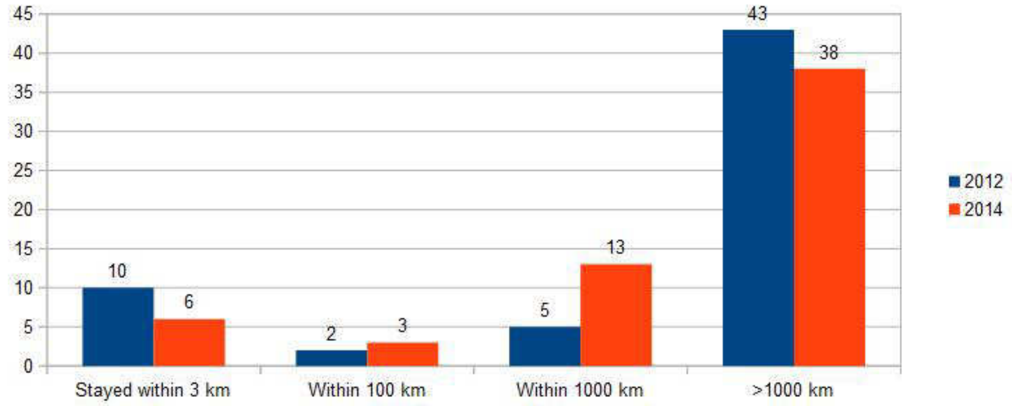

Figure 1.2 - Number of males in each year and distance travelled during breeding season.

Kempenaers and Valcu (2017) provided evidence to support this argument, including:

a) Males did not differ in their condition between early and late in the breeding season;

b) The probability of siring at least one offspring was not completely related to length of stay (tenure) at one site.

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[3] The birds would have flown between 7 to 14 000 km during the spring migration (Kempenaers and Valcu 2017) (appendix 1B).

Together this evidence suggests that males who move are not failed breeders as is traditionally thought, but that sexual selection has promoted males who compete for females "around the clock" (ie: compete intensely in one site and fly long distances to do the same at other sites).

A physiological difference was found in the male blood haematocrit levels (ie: proportion of red blood cells), which determine aerobic performance (Kempenaers and Valcu 2017).

1.4. NAVIGATING BACKWARDS

Ants, like Cataglyphis, are renowned for their navigational skills, as individuals wander through the dry and hot desert habitat. Once food is found, they return immediately back to the nest in a direct path (beeline). They are guided by mainly by "path integration", which depends on the angles moved and distance travelled, based on a specialist area in the eye (to perceive polarised light pattern) and signals from the legs (of distance travelled - "odometer"). Other cues like wind, visual, olfactory, tactile, vibrational, and magnetic (appendix 1C) may be used (Pfeffer and Wittlinger 2016).

But moving backwards is different. "During backward locomotion, the odometer has to deal with unsteady motion and irregularities in inter-leg coordination. The legs' sensory feedback during backward walking is not just a simple reversal of the forward stepping movements: compared with forward homing, ants are facing towards the opposite direction during backward dragging. Hence, the compass system has to cope with a flipped celestial view (in terms of the polarisation pattern and the position of the sun) and an inverted retinotopic image of the visual panorama and landmark environment. The same is true for wind and olfactory cues" (Pfeffer and Wittlinger 2016 p2119).

Schwarz et al (2016) investigated this problem with the desert ant Cataglyphis velox, near Seville, Spain. The researchers built barriers around an active nest in order to control the movement to and from a feeder site. Ants experienced at navigating the route were tested in different conditions.

In the first test, individual ants were given a small or large piece of food before having to negotiate an unexpected 90° turn along their familiar route. Ants with the small piece of food could walk forward, but the large piece of food made those ants walk backwards. It was observed that the "backward-walking ants behaved similarly whether released on their familiar route or in a completely unfamiliar location... [which] suggest that they are uninfluenced by the learned scenery of the route" (Schwarz et al 2016 p401).

In the second test, ants close to returning to the nest with food were moved further along the route and given a small or large piece of food. The backward-walking ants behaved as if they were using celestial compass memory rather than visual cues. Some of these ants were moved to an unfamiliar site. The forward-walking ants quickly adjusted and used their memory of terrestrial cues to find the nest (appendix 1D). "Backward-walking ants, however – as before – did not move in the correct home direction but instead walked in the feeder-to-nest compass direction and maintained that direction when the visual scenery was revealed. That is, they failed to use the visual scenery to correct their heading toward the nest" (Schwarz et al 2016 p403).

Evidence of the use of celestial cues by backward-walking ants was confirmed by introduction of a mirror to change the perceived position of the sun. "As soon as the sun was mirrored, backward-walking ants displayed a turn and moved in a different direction" (Schwarz et al 2016 p404).

1.4.1. "Bandits"

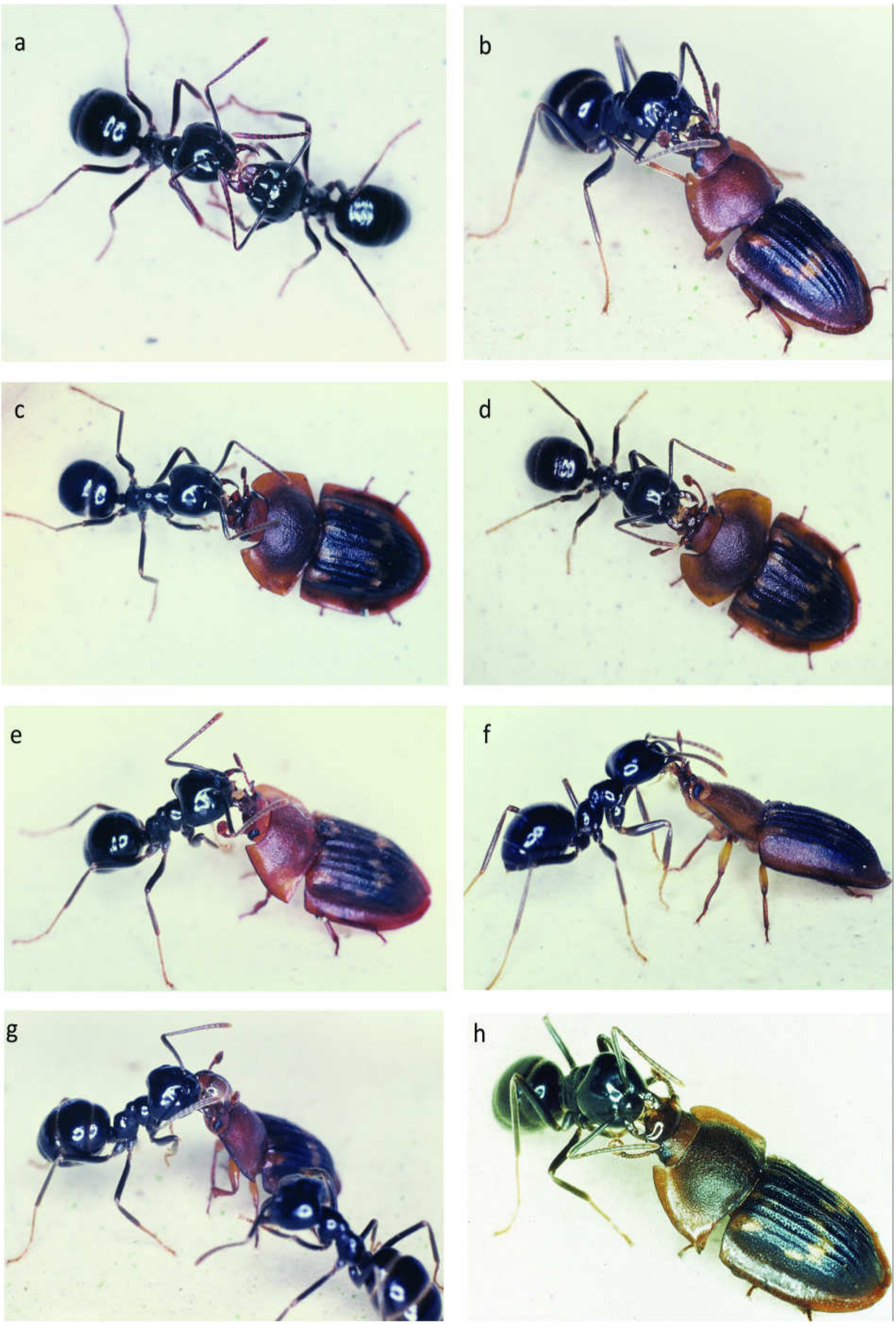
The foraging trails of the central European "shining black ant" (Lasius fuliginosus) are long and complex. They are marked by trail pheromones, and ants move along them day and night between March and October. The ants collect food items including honeydew from aphids (which is swallowed and regurgitated at the nest).

These foraging trails are frequented by other insects who find food as scavengers, prey-robbers ("highwaymen", "bandits"), or as predators of the ants.

An example of a prey-robber is a beetle (Amphotis marginata) who is able to elicit regurgitations from ants (figure 1.3). Holldobbler and Kwapich (2017) reported observations from laboratory and natural colonies in Germany.

It was calculated that a beetle took on average about a quarter of the food carried in the ant's stomach. When tested with other similar ants, the beetles were less successful in gaining food.

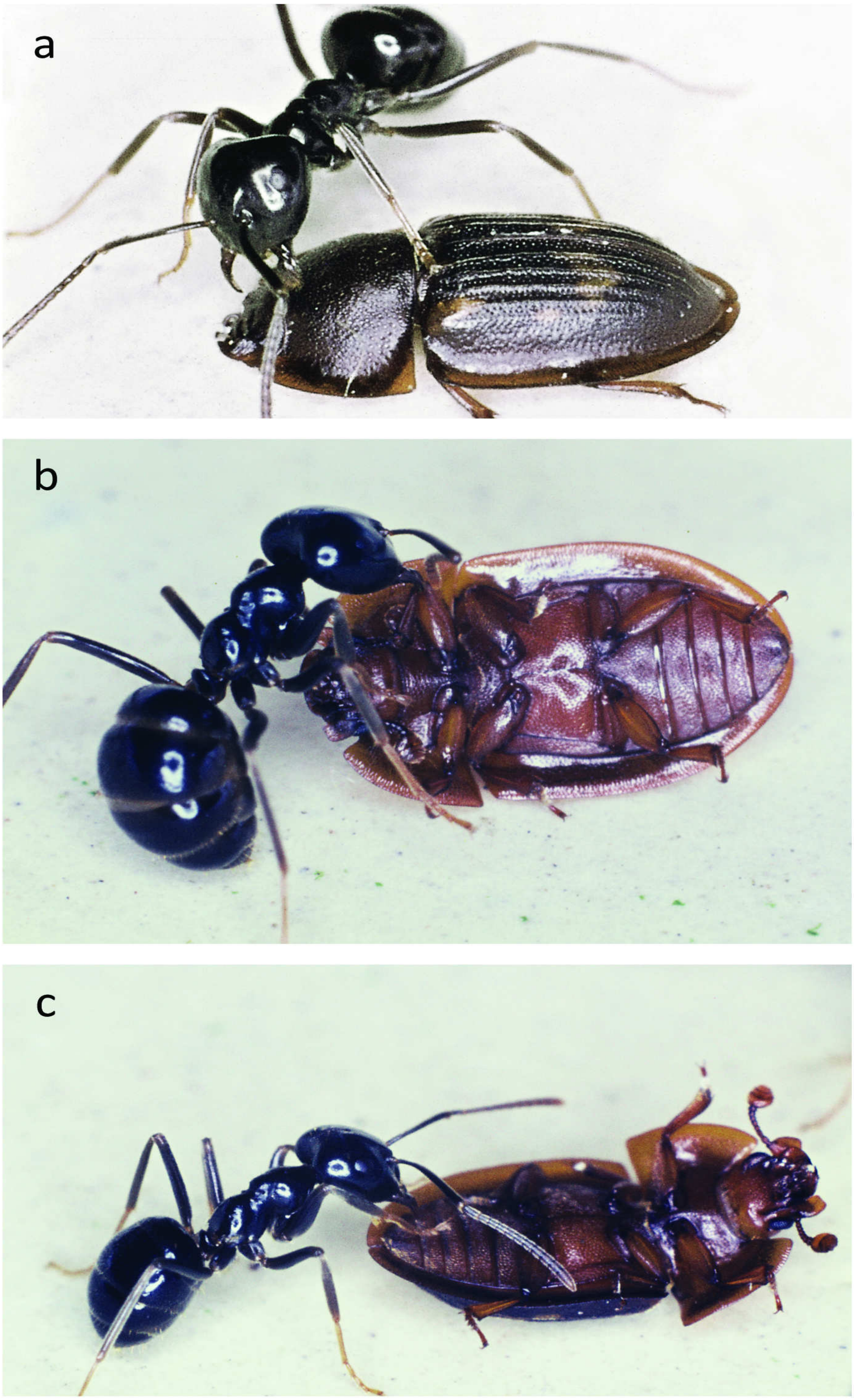
Holldobbler and Kwapich (2017) looked at the body of the beetle under an electron microscope, and it appears to have a head and mandibles that mimic the ants (as well as the use of olfactory cues). Beetles that do not succeed in their mimicking behaviour are attacked by the ants (figure 1.4).



(a-b = food exchange between two ants; c-h = beetle mimicking another ant to elicit food)

(Source: Holldobbler and Kwapich (2017) figure 9)

Figure 1.3 - Eliciting food from the ants.



(Source: Holldobbler and Kwapich (2017) figure 19)

Figure 1.4 - Beetle attacked by ant when mimicking behaviour of former fails.

1.4.2. Walking Backwards

Ants walking backwards have been observed to use "peeking behaviour" (or "winding foodless search loops") (Pfeffer and Wittlinger 2016). The ants would drop the food and turn around, move forward a few steps, and then resume pulling the food backwards in the correct direction. "Such a need to turn around and face the route direction supports the idea that obtaining directional information from terrestrial cues is an egocentric process, where ants must align their view to match their egocentric memories of the visual landscape. Crucially, however, the direction obtained by this egocentric process while facing forward can subsequently be maintained while going backward. Thus, ants must somehow be able to transfer the directional information based on terrestrial cues into a different frame of reference..." (Schwarz et al 2016 p403).

Pfeffer and Wittlinger (2016) conducted their experiments in Tunisia with Cataglyphis fortis ants and a feeder placed ten metres south of a nest entrance. Twenty-six ants who were experienced navigators were given a large food item that required backward-locomotion to drag it. These individuals covered a similar distance in returning as forward walking individuals, suggesting that they were "able to estimate the homing distance correctly" (Pfeffer and Wittlinger 2016 p2122).

In terms of directional accuracy, the backwards ants took a slighter wider angular deviation than forward ants when placed randomly away from the nest.

Pfeffer and Wittlinger (2016) described their observations: "Some ants grasped the food item and started the homing journey immediately with reversed locomotion. Some ants were obviously motivated to drag the food item but were not able to hold it properly at first. They walked around it and probed for a suitable position to grasp and to drag the food. Although we did not quantify this, we did not observe any systematic initial body turns that could be interpreted as orientation behaviour... Remarkably, no ant moved in the incorrect direction, not even within the first few centimetres of homing. All ants at some point interrupted their straight homing path, laid down their food item and performed winding foodless search loops" (p2122).

1.5. FLYING

How do birds avoid colliding when flying towards each other? Based on experiments with male budgerigars in a wind tunnel, Schiffner et al (2016) observed two rules - each bird veers to its right, and each bird changes its latitude relative to the other bird.

For night travellers the stars are orientation references, particularly the starry sky's centre of rotation (eg: indigo bunting) (Foster et al 2018).

Non-flying species studied include (Foster et al 2018):

- Harbour seals and orientation to an individual star.
- Dung beetles and patterns of lunar skylight.

1.6. APPENDIX 1A - "SHAM MATINGS"

A male who mates with multiple females directly increases his number of offspring (ie: more eggs fertilised), but "the number of offspring does not increase for females when mating with multiple males because it is determined by their fecundity. However, multiple mating of females is widespread in a variety of animal taxa..., and sometimes females even actively seek different partners" (Yamazaki and Koizumi 2017 p237).

The female Siberian brook lamprey (Lethenteron kessleri) mates with many males despite the increased predation risk of spawning aggregations, and the energetic costs of a longer spawning period. More than that, Yamazaki and Koizumi (2017) observed many "sham matings" where females did not release their eggs during mating.

The researchers proposed two possible hypotheses for the behaviour:

i) The physical constraint hypothesis - After egg release, there is a time required to prepare the next set of eggs, and "sham mating" speeds up this process somehow.

ii) A female choice hypothesis - Females control the release of eggs based on male quality, number of males present, and surrounding conditions, say.

Yamazaki and Koizumi (2017) tested these hypotheses in two experiments. In the first experiment, one female and three males were placed together in five trials, and in the second experiment, one male and one female were together in ten trials. It was predicted that sham matings should not be evident in the second experiment because there was no opportunity for mate choice.

In total, mating behaviour was observed an average of 77 times per trial, and on average 66% of these were sham matings. There were more sham matings in Experiment 1 (87 vs 44 per trial). Egg release was observed in some consecutive matings [4]. "Both physical constraint and female choice hypotheses were partially supported, although not conclusively" (Yamazaki and Koizumi 2017 p242).

1.7. APPENDIX 1B - VERY LONG-DISTANCE MIGRATION

Bar-tailed godwits (Limosa lapponica) (figure 1.5) migrate very long distances. Between 2006 and 2010, Battley et al (2012) tagged thirty adults with an implantable satellite transmitter.

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

Figure 1.5 - Bar-tailed godwit.

Twelve of them were tagged northwards from New Zealand (Firth of Thames and Golden Bay) through eastern China (Yellow Sea region) to the Russian Far East (eg: Yakutia area) and Alaska (eg: Yukon-Kuskokwim Delta) (over 10 000 km). Eight of these birds were tracked on the southwards return non-stop across the Pacific (through the Hawaiian Islands area) (figure 1.6). Each flight took at least one week of flying.

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[4] To support the physical constraint hypothesis, females should not be able to release eggs in consecutive matings.

(Source: US Geological Survey; in public domain)

Figure 1.6 - Flight of satellite-tagged godwits from another study showing general pattern of migration.

1.8. APPENDIX 1C - MAGNETIC SENSE

How is the magnetic field used by animals generally? Qin et al (2016) reported the discovery of a protein in animal cells that forms a structure with iron atoms that responds to the Earth's magnetic field (known as a "magnetic protein biocompass"). But Winklhofer and Mouritsen (2016) argued that the structure would be "too weakly magnetic to sense Earth's field" (Cyranoski 2017 p17).

Determining one's east-west position (the longitude problem) has been observed in experienced night-migratory songbirds. Chernetsov et al (2017) reported that experienced adult Eurasian reed warblers (Acrocephalus scirpaceus) used magnetic declination [5] under clear skies to solve the longitude problem.

Fifteen experienced adults and 25 first-time migrators were captured in Rybachy, Russia, and placed in cages with a rotated magnetic field. The birds'

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[5] This is the angle between magnetic north and true north.

spontaneous night-time migration orientation was recorded. The artificial magnetic field gave the impression that the birds were west-north-west of their normal migration route. Only the experienced birds could adapt their flight orientation.

When distinguishing between a biochemical basis to magnetoreception or the mineral magnetite, a strong, short magnetic pulse has been used in experiments. This is expected to disrupt the mineral, but not the biochemical process in subsequent orientation behaviour. For example, Caribbean spiny lobsters showed disorientation (Ernst and Lohmann 2016), which supports the magnetite-basis to magnetoreception (Fitak et al 2017).

Fitak et al (2017) used this methodology with rainbow trout. Increased expression of ferritin [6] was found in the fish after exposure to the magnetic pulse, and this finding is "consistent with the hypothesis that ferritin is involved in generating or repairing magnetite-based magnetoreceptors" (Fitak et al 2017 p4).

1.9. APPENDIX 1D - MEMORY

What is the physical memory trace (known as the engram)? The traditional view is the modification of synaptic connections between cells in the brain (eg: Takeuchi et al 2014).

Bedecarrats et al (2018) proposed an alternative idea that long-term memory is encoded by epigenetic changes to DNA via non-coding RNAs. If this is the case, then it may be possible to transfer RNA from one individual to another (ie: "memory transfer").

Bedecarrats et al (2018) showed this possibility with the marine mollusc, California sea hare (Aplysia californica). Adults learned that a touch from a probe caused a mild electric shock, and RNA was extracted from their central nervous system and injected into untrained individuals, who showed some response in neurons to the probe. In other words, individuals who had not learned that the probe caused a shock showed some reaction to the probe.

Working with laboratory rats, Lay et al (2018) showed protein synthesis in the amygdala for fear memories (ie: epigenetic processes). Over 300 adult rats were conditioned to associate a particular chamber (neutral stimulus) with a mild electric shock to the foot (first-order conditioning), and once this was learned,

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[6] Ferritin is a protein that stores iron within cells (Fitak et al 2017).

another neutral stimulus (eg: light on) was associated with the electric shock (second-order conditioning). There were physiological differences found between the first- and second-order conditioning.

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2. VISION IN DIM LIGHT

2.1. INTRODUCTION

It is now known that "many nocturnal animals see the world more or less in the same manner as their day-active relatives. Many are able to see colour, to use optic flow cues to control flight, and to navigate using learned visual landmarks and celestial cues such as polarised light" (O'Carroll and Warrant 2017 p1).

Nocturnal and deep-sea habitats are "perishingly dark places" (O'Carroll and Warrant 2017). Light is so much less at night (eg: full moon light is one million times dimmer than full sunlight and starlight is 100 million times dimmer) (O'Carroll and Warrant 2017). In the sea, no daylight penetrates below 1000 metres [7] (O'Carroll and Warrant 2017), and downwelling sunlight decreases by 1.5 orders of magnitude every 1000 metres in clear sea water (Thomas et al 2017).

"Thus, on a starlit night or in a deep ocean, vision is relentlessly pressed at the limits of the physically possible. While some species have given up the fight altogether, with their eyes having regressed to mere vestiges of their counterparts in bright habitats, in others the eyes have evolved extreme adaptations for extracting the most fleeting of visual cues. Indeed, in the world's dimmest habitats– terrestrial or aquatic – many animals depend on good vision to survive" (O'Carroll and Warrant 2017 p3).

This means that the visual system of animals in these habitats has adapted: "Optical adaptations improve the visual image by gathering more photons into the image formed on the retina, improving the ability to distinguish subtle contrasts, whether these be in luminance, colour or in the e-vector of polarised light. Equally important, neural adaptations allow the brain to adjust the way in which information gathered by the retina is processed–pooling signals over time or from neighbouring detectors to improve reliability, albeit at the expense of resolution in time or space" (O'Carroll and Warrant 2017 p4) (table 2.1).

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[7] The mesopelagic region (200 - 1000 m depth) (Thomas et al 2017).

Animal	Focal length (mm)	Adaptations
Shark	9.2	Many more rods than cones
Owl	17.3	Equal rods and cones
Cat	12.8	More rods than cones

(After Bradbury and Vehrencamp 1998)

Table 2.1 - Three examples of eye adaptations for dim light [8].

2.2. NOCTURNAL INSECTS

Warrant (2017) observed: "Insects and other arthropods are capable of extraordinary behavioural feats, seemingly disproportionate in sophistication compared with their small bodies and tiny brains" (p1). He used the visual behaviours of nocturnal insects as an example of this point. For example, the tropical nocturnal sweat bee (Megalopta genalis) navigates through dense rainforest in a light level of five photons absorbed by each photoreceptor every second (Warrant 2017) [9] [10].

Insects are aided here by compound eyes which are highly sensitive to light, and specialised adaptations in the retina and optic lobe of the brain. However, "the remarkable visual performance of nocturnal insects cannot entirely be explained by our current understanding of their eyes and their optic lobes. As yet unknown neural circuits, both within the optic lobes as well as in other areas of the brain, are undoubtedly of vital importance for improving visual performance to the levels revealed by behaviour" (Warrant 2017 p2).

Warrant (2017) distinguished three sources of "noise" (photon shot, transducer, and dark) that make vision in dim light difficult. These are aspects of the physiological system that can "contaminate or even drown" a weak visual signal. "Dark noise", for example, is where, in the visual system, "the biochemical pathways responsible for transduction are occasionally activated, even in perfect darkness" (Warrant 2017 p4) [11].

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[8] Studying sharks is not easy in many aspects, like their age (appendix 2A).

[9] It has been estimated that "approximately 100 photons at the cornea with a spot size covering 100-1000 rod photoreceptors was sufficient for a human observer to see the flash of light" (Field and Sampath 2017 p2).

[10] One solution is "slower vision" (ie: slower response firing time of cells) (Warrant 2017).

[11] Keeping the senses sharp is crucial (appendix 2B).

2.3. DEEP SEA

Thomas et al (2017) reported the case of cockeyed squids where the left eye is twice the diameter of the right eye, different pigments filter the light in each eye, and the left optic lobe can be twice the size of the right.

The researchers reviewed 25 years of deep-sea video footage of two species of these squids. The larger eye was found to be oriented upwards to pick up downwelling light and the smaller eye was oriented downwards.

de Busserolles and Marshall (2017) quoted the example of lanternfishes, which have visual adaptations that increase light collection in the eye (eg: pure rod retina [12]), giving a light sensitivity that is 10-100 times that of humans. But the trade-off is very poor visual acuity (eg: visual recognition of objects).

There are over 250 species of lanternfishes and they all emit bioluminescence (de Busserolles and Marshall 2017).

2.4. APPENDIX 2A - AGE OF SHARKS

Establishing the age of sharks, for example, traditionally involves counting the pairs of bands inside the spine when died, which were assumed to be like rings of a tree (Cressey 2017). However, this method may underestimate the age, argued Harry (2018), who used other methods. One method was chemical marking, which involves injecting the shark with a fluorescent dye that is taken up in the spine, and can show the amount of growth when the animal is recaptured (Cressey 2017). But this does depend on capturing the individual twice.

"Reproductive senescence" (RS) is "the decline in reproductive success with increasing age" (Lemaitre and Gaillard 2017 p2182).

"Reproductive machinery" has a role to play, particularly for females, as their "reproductive physiology is extremely complex... and the depreciation of many aspects of the reproductive system might compromise reproductive success, such as the pattern of hormone secretion or atrophy of the oviduct... The decrease of most reproductive functions can generally be explained by general dysregulation of the pituitary–hypothalamic–ovarian axis" (Lemaitre and Gaillard 2017 p2186).

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[12] The human retina, for example, has rods and cones, where the cones are activated by daylight and the rods by nighttime low light.

For males, loss of sperm quantity and/or quality are important (Lemaitre and Gaillard 2017). Lemaitre and Gaillard (2017) pointed out that "although reproductive senescence is generally studied only from the female viewpoint, age-specific female reproductive success strongly depends on male–female interactions. Thus, a reduction in male fertilisation efficiency with increasing age has detrimental consequences for female fitness" (p2182).

Variations in environmental conditions can also have an influence (Lemaitre and Gaillard 2017). For example, female red deer born at times of high population density have an accelerated RS (Nussey et al 2007).

2.4.1. Ageless?

Ruby et al (2018) reported that naked mole rats in the laboratory did not show an increased risk of dying as their aged, which is the opposite of typical mammalian biology. The Gompertz law states that the risk of dying increases with age (eg: humans - the risk doubles every eight years after 30 years old) (Kupferschmidt 2018). The naked mole rat was estimated to have a 1 in 10 000 chance of death at six months old (sexual maturity) and the same risk fifteen years later (Kupferschmidt 2018).

But the sample of captive animals on which the calculations were made was small, argued critics (Kupferschmidt 2018).

2.5. APPENDIX 2B - AGE-RELATED HEARING LOSS

Age-related hearing loss (presbycusis) occurs in many mammals, including humans and mice, but not in birds like the barn owl (Tyto alba) (Krumm et al 2017).

Krumm et al (2017) tested four "young owls" (less than 2 years old) and three "old owls" (older than 13 years) hand-reared in Germany. The birds had been trained to respond to certain tones and not others to receive a food reward (a Go/NoGO paradigm). Tones were played at different volumes from a loudspeaker in a sound-proof chamber.

The threshold of hearing was similar for both groups (with the young owls being non-significantly more sensitive).

The owl is nocturnal and relies on auditory cues for hunting, though many birds die in the first year "probably... from a lack of experience in locating and catching prey and the low abundance of prey" (Krumm et al 2017 p5).

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3. ANIMAL COLOURATION AND SEXUAL SELECTION

3.1. COLOUR

"Colour in nature is remarkably diverse and often visually stunning. It is produced by both chemical pigments, which absorb certain wavelengths of light, and by physical structures on the scale of hundreds of nanometres, which manipulate light in varied ways" (Caro et al 2017 p2).

Colour signals and colour vision co-evolved. "Co-evolution is potentially important in speciation, and could also affect the efficacy and honesty of communication, especially when signallers and receivers have conflicting interests" (Lind et al 2017 p1).

Butterflies, for instance, have visual photoreceptors for perception of a number of different colours, while birds have much more limited colour vision. But there is also great variety between species, and between the sexes of the same species (Lind et al 2017).

Colour in nature is being studied to aid the production of artificial materials (known as biomimetics). Notable examples in nature include (Caro et al 2017):

- Hercules beetle (Dynastes hercules) - changes colour with varying humidity.

- Helmet gecko (Tarantola chazaliae) - possesses colour cones in the eye that 350 times more sensitive than human.

- Peacock mantis shrimp (Odontodactylus scyllarus) - has a special type of photoreceptor in the eye that can see polarised light.

- Bornean gliding lizard (Draco cornutus) - matches skin colour to freshly fallen leaves in rainforest (appendix 3A).

3.2. FLUORESCENCE

Fluorescence involves the absorption of shorter-wavelength light by a protein (excitation) , for example, and the release of some of that absorbed energy as longer-wavelength light (emission). In most cases, blue or blue/green light is the excitation, and green, yellow or red fluorescence is the emission (Marshall and Johnsen 2017).

Marshall and Johnsen (2017) proposed a number of questions related to fluorescence as visual communication rather than as a byproduct of a pigment:

a) Is the fluorescence on a visible part of the body?

b) Can the fluorescence be seen by the conspecifics (ie: appropriate visual wavelength)?

c) Is the fluorescence visible in the animal's normal light conditions?

d) What behaviours would benefit from fluorescence?

Common examples of fluorescence include (Marshall and Johnsen 2017):

- Mantis shrimp (Lysiosquillina glabriuscula) - yellow fluorescent markings on body parts prominent in conflicts and mate choice.

- Jumping spiders (eg: Cosmophasis umbratica) - Male fluorescent palps important in mate choice.

- Budgerigar (Melopsittacus undulatus) - fluorescent yellow crowns and mate preference. In an experiment, Arnold et al (2002) used sunblocker on the fluorescent area of half of the birds, and both males and females showed less mate preference for these individuals compared to normal birds.

3.3. SEXUAL SELECTION

Sexual selection "arises from mating or fertilisation advantages that individuals of the chosen sex, usually males, gain from bearing attractive ornaments (inter-sexual mate choice) or other traits that enhance success in competition for mates or limiting resources that attract mates (intra-sexual mate competition)" (Romano et al 2017 p1583).

Romano et al (2017) produced a meta-analysis of studies on sexual selection in the barn swallow (Hirundo rustica) (figure 3.1) [13]. This bird is socially monogamous, but with extra-pair copulations. Variations in plumage are influenced by sexual selection, including tail feather length, tail feather asymmetry, size of white spots on tail feathers, and throat patch colour and size.

Sexual selection was expected to be a stronger pressure on males than females [14], but "the fitness of both sexes was positively affected by carrying large sexually selected traits" (Romano et al 2017 p1594). However, overall reproductive success (eg: total number of eggs and nestlings produced per breeding season) did vary with intense selection pressure at the start of the breeding season - ie: "earlier arrival from migration, mating and laying for highly ornamented individuals, which therefore have more broods per season than less ornamented ones" (Romano et al 2017 p1595).

It was also found that "sexual selection on different plumage ornaments varies among geographically distinct populations.

3.3.1. Genitalia

The genitalia of male animals with internal fertilisation evolve rapidly and faster than other physical characteristics (Eberhard 1985). Sexual selection is the driver of this process through cryptic female choice (eg: a preference for genitalia that fit better) or sexually antagonistic co-evolution (to combat female evolution related to reproduction) (Klaczko et al 2015).

In a study of 25 species of Caribbean Anolis lizard, Klaczko et al (2015) estimated that the male genitalia (known as hemipenes) had evolved around six times faster

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[13] Four migrating sub-species have been distinguished: Hirundo rustica rustica (found in Europe, North Africa and Western Asia), Hirundo rustica erythrogaster (North America and Argentina), Hirundo rustica gutturalis and Hirundo rustica tytlen (both in Asia), and two non-migratory sub-species: Hirundo rustica savignii (in Egypt), and Hirundo rustica transitiva (Middle East) (Romano et al 2017).

[14] Evolution does not always do what is predicted (appendix 3B).

(Source: Andreas Eichler CC-BY-SA 4.0 wikimedia)

Figure 3.1 - Barn swallow.

than three other body parts.

3.3.2. Female Birdsong

Female birdsong has traditionally been viewed as less common than that of males, mainly because it was believed to have no adaptive function (eg: Nice 1943). But it appears in "conditions involving long-term territoriality and high competition for mates and resources" (Reichard et al 2018).

Reichard et al (2018) studied the Dark-eyed Junco (Junco hyemalis) (figure 3.2), where female song had been reported previously as absent or rare. The exception was experimentally increased testosterone females whose song resembled that of males (Ellen D Ketterson personal observation in Reichard et al 2018).

In an experiment with a wild population of Juncos in San Diego, three of seventeen paired females produced male-like song early in the breeding season (pre-nesting) when presented with a live, caged female. The pre-nesting stage of the season is the time of the highest levels of circulating testosterone in the females. This "suggests a role for testosterone in promoting female song", and in the context of intrusion from a rival female in this socially monogamous species (Reichard et al 2018).

(Source: David Monniaux)

Figure 3.2 - Dark-eyed Junco.

3.4. COURTSHIP SIGNAL

As much as the courtship display itself, its repetition, which is energetically costly, is a signal of quality. "This heavy investment in signal production is likely to allow females to select physically fit mates as these 'signals of stamina' will reflect a male's ability to perform other demanding activities associated with survival, and reduce the risk of mating with weaker signallers that might be diseased or parasitised" (Mowles et al 2018 p1).

The display rate of courtship signals is also important. Female fiddler crabs, for example, prefer males who wave their enlarged claw faster than rivals (Murai and Backwell 2006). But the display rate changes during the courting interaction. The signal may start slowly and speed up as the female needs more encouragement to mate, then slow down with fatigue. How much attention does the female pay to the changes in speed? Mowles et al (2018) investigated this question in fiddler crabs with "replica robot males" which mimicked the claw waving signal.

One hundred and fifty-five female crabs captured in Darwin, Australia, were used in three independent experimental conditions:

i) Escalation choice trial - A choice between a robot male whose waving speed escalated over ninety seconds, and a constant speed robot.

ii) De-escalation choice trial - Waving slowing down vs constant speed.

iii) Three-choice trial - A choice of three males: escalating, de-escalating, and constant speed.

The escalating male was chosen significantly more often, particularly the longer time that had passed. "This demonstrates that females are sensitive to changes in rate and that when signal rates are perceptibly changing among the males in a group, females select the ones that are escalating..." (Mowles et al 2018 p3).

3.4.1. Brain Size

Mate-quality recognition is a cognitive ability involving the processing and retention of information. For example, the choosy sex must be able to recognise the sexual traits and behaviour, and retain that information for comparison of individuals. "Variation in cognitive ability is often directly influenced by brain size and has been suggested to strongly influence variation in sexual behaviour at the individual and species levels" (Corral-Lopez et al 2017 p1).

Corral-Lopez et al (2017) showed the relationship between female brain size and assessment of male attractiveness among guppies (Poecilia reticulata). Females of this fish species prefer males with more ornamental colouration and larger tails.

Thirty-six large-brained and 36 small-brained females from the fifth generation of selective breeding for brain size were used in this experiment. They were presented with an attractive and an unattractive male, each at either end of a tank (dichotomous choice preference test) for fifteen minutes, and where the female stayed was her choice. Large-brained females showed a significant preference for attractive males, whereas small-brained females showed no preference.

The researchers commented: "Constraints in cognitive abilities might thus limit the capacity of an individual to perform optimal quality assessment when selecting a sexual partner. If there are fitness benefits to the female for mating with attractive males, female cognitive ability might be under considerable selection to ensure optimal decision-making in mate choice. The huge variation in brain anatomy and cognitive abilities found within and across species suggests that these selection pressures for increased cognitive ability could counter the extensive costs associated with growing and maintaining a large brain, and explains the substantial genetic variation observed in brain size among animals" (Corral-Lopez et al 2017 p4) (appendix 3D).

3.5. POST-COPULATION STRATEGIES

3.5.1. Anti-Aphrodisiac Pheromones

In species where females mate with more than one partner, an individual male will try to guarantee his paternity with post-copulation strategies, like mate guarding or via the ejaculate (last-male sperm precedence) (Malouines 2017).

In the latter case, ejaculates can include additional substances to sperm, and these may neutralise previous sperm, or prevent future sperm from reaching the eggs (chemical plugs). There are also anti-aphrodisiac (AA) pheromones, which are substances in the ejaculate that make the female unattractive to subsequent males for a period of time (Malouines 2017) [15].

Andersson et al (2000), for example, experimentally applied AA pheromones to virgin female pierid butterflies, and males did not try to mate with them.

Happ (1969) was the first to report an AA pheromone in the yellow mealworm beetle (Tenebrio molitor), and these pheromones are now documented in fourteen genera (mostly insects with the exception of garter snakes, but not all species in each order use them) (Malouines 2017).

Chemically, the AA compound is often the same as the male's smell, which is "less costly and easier to evolve than the use of a new chemical" (Malouines 2017 p1576).

The benefits of AAs to males are to stop future female matings, but also as a signal of previous matings. For example, in the green-veined white butterfly (Pieris napi), males produce ejaculates that are about one-

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[15] AAs can be transmitted in cuticular contact, or in the spermatophore (nuptial gift) (Malouines 2017).

quarter larger when mating with AA pheromone-smelling females than virgins (Larsdotter-Mellstrom et al 2015).

Females may benefit also from AAs because they "have a refractory period after mating. In this case, it is advantageous for them to have an honest signal of their mating status that will reduce harassment from males, therefore saving females time and energy" (Malouines 2017 p1578). This is especially so for garter snakes.

Another benefit is in species where mating damages the female's body (eg: fruit fly; Drosophila melanogaster) as it allows "females to avoid unnecessary matings and the ensuing internal damage" (Malouines 2017 p1578).

Female "stink clubs" to share the AA have been reported in the red postman butterfly (Heliconius erato), yet this same species suffers the cost of less spermatophore and its nutrients by mating once (Malouines 2017).

Both sexes face the cost of AAs chemically attracting parasites.

3.6. WEAPONS

Males have adornments/ornaments which are attractive to females, and "an arsenal of outgrowths that function in male-male combat (weapons)" (Emlen 2008 p388).

Emlen (2008) argued that weapons evolve when their benefits outweigh the costs, and in situations where critical resources can be defended by dominant individuals. Examples of critical resources include burrows or tunnels (appendix 3C) where females lay eggs and the male can guard the entrance, or food sources (eg: rhinoceros beetles guard tree trunks where sap oozes) (Emlen 2008).

Weapons are also an honest signal to both females and other males of the individual's condition or quality as "it would not pay a small male to cheat by producing a mismatched weapon, because these males would be challenged repeatedly by rivals and quickly discovered as charlatans" (Emlen 2008 p404). It is noted that the "most elaborate weapons rarely inflict real damage to opponents, but these structures are very effective at revealing even subtle differences among males in their size, status, or physical condition [e.g., rhinoceros beetle horns... In contrast, many animals with unimpressive or even inconspicuous weapons regularly inflict serious damage in male contests..." (Emlen 2008 p405).

Emlen (2008) described six possible mechanisms for the evolution of different weapons in different species:

1. Weapons gradually changed from fighting assets to

signals of quality.

2. Weapons changed from armaments for real fights to structures for ritualised contests (eg: locking horns to assess the opponent rather than to injure them).

3. Differing habitats influenced the development of different weapons.

4. An "evolutionary arms race" where better weapons gave the possessor an advantage in contests.

5. Some weapons evolved because they are less costly than others.

6. The volatility of sexual selection.

3.6.1. Defence

Reef fishes known as fangblennies have venom in enlarged canine teeth, which is used for defence. When inside the mouth of a predator, the venom causes the predator to reject the fangbleeny unharmed (Casewell et al 2017).

"Indeed, the use of an oral venom system exclusively for defensive purposes is unusual in the animal kingdom" (Casewell et al 2017 p1185).

Losey (1972) studied the poison-fanged blenny (Meiacanthus atrodorsalis) in detail. When the fangs were removed, the fishes were readily consumed by predators, but rejected when the fangs were present.

3.7. DIVORCE

Returning to the same mate every breeding season has advantages in terms of less time and energy spent in finding a new mate and establishing a new pair bond, and in co-ordinating parental behaviour. Faithful bird pairs generally, for instance, have higher reproductive success (Gilsenan et al 2017).

But divorce, "where one or both individuals from a previous breeding pair form a new pair with another individual while their former partner is still alive" (Gilsenan et al 2017 p57), is quite frequent. One explanation is that one member of the pair gains benefits that outweigh the costs of mate change (eg: gain higher quality mate or a more compatible mate). This is the "better option" hypothesis (Ens et al 1993).

Other reasons for divorce include differences in arrival time of pair members at the breeding site ("musical chairs" hypothesis; Dhondt and Adriaensen 1994), or separation outside the breeding season ("accidental loss" hypothesis; Owen et al 1988). There is also intra-sexual conflict which "can lead to a new male or female talking over a territory/mate, with passive acceptance of the usurper as the new breeding partner" (Gilsenan et al 2017 p58).

Gilsenan et al (2017) explored these different theories in a study of divorce in a nestbox-breeding population of blue tits (Cyanistes caeruleus) in Westerholz, southern Germany. Data were available from 2007 to 2015. The nestboxes recorded entries and exits of birds automatically, while researchers manually checked egg clutches and trapped the adults regularly.

On average, two-thirds of blue tits divorced each year (of 60 - 100 breeding pairs). Females paired with divorced males started to lay about two days later than faithful females, and laid about half as many eggs.

Divorce was not related to previous breeding success. "The only significant predictor of divorce was the difference in arrival time to the study site between the members of... pairs... Faithful pairs were more likely to arrive simultaneously at the breeding site" (Gilsenan et al 2017 p64). Asynchrony in arrival time may be due to pair members spending the winter with different flocks. So, divorce is a by-product of this behaviour rather than an active decision for these birds. This fits with the "musical chairs" or "accidental loss" hypotheses rather than the "better option" hypothesis.

3.8. APPENDIX 3A - CAMOUFLAGE

"For camouflage to succeed, an individual has to pass undetected, unrecognised or untargeted, and hence it is the processing of visual information that needs to be deceived. Camouflage is therefore an adaptation to the perception and cognitive mechanisms of another animal" (Merilaita et al 2017 p1).

Camouflage colouration can be used to reduce the visual salience of edges and surfaces, body parts, the whole animal, and even movement. For example, "background matching" (or "generalised resemblance" or "background picturing") makes it difficult for the viewer to distinguish the animal from the background, while eyespots or "divertive markings" visually distract the viewer, and "dazzle" (high-contrast geometric surface patterns) distorts the perceived speed of movement (Merilaita et al 2017) [16].

In the case of divertive markings. predators often

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[16] Movement and striped colour patterns can create camouflage or conspicuousness. For example, striped patterns parallel to the direction of motion in racing snakes conceal motion, but movement in the opposite direction from the striped pattern is highly visible (Bradbury and Vehrencamp 1998).

use the location of the head of the prey as an indicator of the direction of escape or as a vulnerable area. "Therefore, distorting that information can increase the prey's chance of surviving an encounter with a predator" (Merilaita et al 2017 p5).

Technically, camouflage works by reducing the visual signal-to-noise ratio. This is the amount of useful visual information (signal) to the amount of irrelevant or false information (noise) (Merilaita et al 2017).

Insects that feed on exposed leaf surfaces are at particular risk of predator without camouflage of some kind. Specifically, with masquerade, the insect looks like another object (eg: early thorn moth caterpillar as a twig; giant swallowtail caterpillar as bird dropping) (Konstantinov et al 2018).

Konstantinov et al (2018) reported "a unique twist to the masquerade strategy" with adult flea beetles that resemble their own leaf-feeding damage (ie: "a non-random correspondence between the colour and shape of the feeding damage and the body size and colour of the beetles that produced that damage"; p315).

Cuttlefish, squids and octopuses (Coleoid cephalopods) are very good at camouflage as their "body colouration, pattern, skin texture and posture are under the direct control of the brain, which enables them to change their appearance in milliseconds" (Okamoto et al 2017 p307). Not only can they match their skin colour to the background, but they can mimic inanimate three-dimensional objects, like rocks and seaweed, and even imitate the appearance and behaviour of other sea animals (Okamoto et al 2017). For example, a mimic octopus (Thaumoctopus mimicus) has been observed to imitate a poisonous sole, sea snake and lionfish (Norman et al 2001).

Okamoto et al (2017) reported a novel arm-flapping behaviour by the pharaoh cuttlefish (Sepia pharaonis). The researchers described the behaviour thus: "The colour and posture of the first pair of arms resembled the eyes of a crustacean, and the movement of their second and third pairs of arms resembled a crustacean moving its appendages. The dorsal mantle of the cuttlefish would correspond to the gastropod shell of a hermit crab" Okamoto et al 2017 p310).

Okamoto et al 92017) argued that "mimicking hermit crabs, which have a hard shell to protect them against predators, presumably would be beneficial to some degree for the cuttlefish. In addition, hermit crabs are generally scavengers and filter feeders... and not active hunters. Thus, mimicking hermit crabs would help cuttlefish to approach their prey more closely, inside the range of their tentacles" (p310).

3.8.1. Acoustic Camouflage

Predators strive to control the cues to their presence for the prey (eg: lions hunt in areas with vegetation to conceal their approach rather in open areas - prey "catchability" areas; Soley 2016). But "some environments are unavoidable and can be especially challenging for predators" (Soley 2016 p2) as in predators that eat web-building spiders (known as araneophagic insects and spiders). These predators must approach across the web without tell-tale vibrations that alert the prey. Strategies of predators to circumvent this problem include jumping spiders that lower themselves onto the prey, or damselflies that pick off the spider while in flight (Soley 2016).

The assassin bug (Stenolemus giraffa), however, approaches its prey on foot across the web. "Breaking threads is dangerous, as it requires direct manipulation of the silk, and hence the production of vibrations. Nevertheless, the breaking of threads commonly appears to go unnoticed by the spiders. This is especially surprising when S. giraffa breaks threads next to the spider. Behavioural observations suggest that S. giraffa lowers the amplitude of vibrations produced when breaking threads by holding on to the loose ends of the broken thread and causing them to sag prior to release" (Soley 2016 p2).

Soley (2016) observed the bugs recklessly break threads occasionally. "Spiders often ignore large-scale disturbances in their webs, such as those caused by wind or falling debris, and one could regard reckless breaking of threads as a self-generated 'smokescreen' tactic [Wilcox et al 1996] used by the bugs to conceal themselves from the spiders. However, the bugs never advanced quickly across the web after using the reckless tactic, a behaviour that would be expected if this tactic constituted a self-generated smokescreen" (Soley 2016 p12). The bugs did, however, break threads in the presence of the wind as "acoustic camouflage".

3.8.2. Predator Mimicry

Mimicry usually occurs in one way (eg: physical appearance or movement), but sometimes there may be mimicry in multiple ways "when the signals are equally salient for prey discrimination [17] or when different predators use different traits for recognising the prey" [18] (Wang et al 2017 p219).

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[17] Explained by the "back-up signal" hypothesis.

[18] Explained by the "multiple message" hypothesis (Johnstone 1996).

Multiple signal mimicry can occur with "predator mimicry" (Zaret 1977), where "the prey resembles its predator to gain protection. This mimicry can be so successful that predators engage in courtship or territorial displays to their potential prey, showing that they misidentify the mimics as conspecifics" (Wang et al 2017 p220). Examples include a wasp-mimicking locust, and caterpillars that chemically mimic ants (Wang et al 2017).

Wang et al (2017) studied two jumping spider mimicking moths (Brenthia coronigera (metalmark moth) and Choreutis hyligenes), which show jumping behaviour when moving on vegetation, and a "peacock-like display". In experiments, spiders attacked less the moths who mimicked both the appearance and movement of the spiders, suggesting support for the "back-up signal" hypothesis.

3.9. APPENDIX 3B - STASIS PARADOX

The "stasis paradox" (Merila et al 2001a) is where evolutionary changes in a population are not observed, though they are predicted. Bonnet et al (2017) offered these possible explanations:

a) Evolutionary changes are masked by short-term changes in the opposite direction. Sometimes called "cryptic evolution" (Merila et al 2001b). For example, evolutionary changes in favour of fat accumulation are masked by food shortages and reductions in fat resources among the population.

b) Evolutionary changes are not necessarily singular but can be correlated as in parent-offspring conflicts. The offspring evolved to be larger which is counterbalanced by "selection against investment per offspring on the level of parents" (Bonnet et al 2017).

3.10. APPENDIX 3C - TUNNELS

The basis of nest-building behaviour in different animals is genetic. This can be seen in breeding experiments with two species of mice in the USA:

- Oldfield mice (Peromyscus polionotus) - dig long tunnels with a branching escape route that ends just below the surface;

- Deer mice (Peromyscus maniculatus) - dig short tunnels for their nests (Dunn 2014).

Weber et al (2003) mated these two species of mice to see what type of tunnels the hybrid offspring would build. It was found that the offspring all built long tunnels with escape branches. "In theory, this pattern could result from simple dominance involving as few as two genes: one associated with tunnel length and the other with the escape hatch" (Dunn 2014 p58).

The researchers then bred the hybrids with oldfield mice (known as a backcross). The resulting offspring built escape routes or not (about half and half), but varied in the tunnel length.

Subsequently, Weber and Hockstra (2009) identified the genes on the mouse genome associated with escape-branch building (one single chromosome area) and tunnel length (genes on three chromosomes). This explained the findings from the backcross experiment, and "demonstrated that even in smart animals, such as mice, complex behaviours involved in nest construction can be both genetically encoded and a product of evolutionary forces" (Dunn 2014 p59).

3.11. APPENDIX 3D - SOCIAL BRAIN HYPOTHESIS

The "social brain hypothesis" (SBH) (Dunbar 1998) explains the evolution of the large primate brain as "an evolutionary response to complex and information-rich social environments" (Fox et al 2017).

Fox et al (2017) applied this theory to cetaceans (whales and dolphins) in a survey of the literature on these species. "Whales and dolphins (cetaceans) have the largest nervous systems of any taxonomic group, and rank highly on every putative measure of neuroanatomical complexity. Many cetaceans are also organised in hierarchical social structures and display an astonishing breadth of cultural and pro-social behaviours, providing a rare parallel to humans and other primates in terms of social, behavioural and neuroanatomical complexity" (Fox et al 2017 p1699).

Ninety species were categorised as usually alone except for specific aggregations ("ephemeral aggregations"), mid-sized associations, or large groups ("mega-pods") (dozens of individuals upwards). Cetaceans in mid-sized social groups had the largest brains in absolute terms, and relative to body size, followed by cetaceans from large communities.

Fox et al (2017) concluded: "Our analyses demonstrate that cetacean brain evolution is best explained by the demands associated with maintaining and co-ordinating cohesive social groups and the advantages of living in such groups; social repertoire is broadest in species found in mid-sized groups with typically strong social bonds, and in those species with the largest brains" (p1701). This supports the SBH.

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4. THE COMPROMISES AND BENEFITS OF GROUP LIVING

4.1. GROUP LIVING

"Most vertebrates, including humans, are gregarious to a certain degree. They tend to form shoals, flocks, coveys, herds, bands, packs, parties or colonies... of conspecific individuals. Conspecifics make up a major component of their environment thereby influencing major aspects of their lives, such as predation pressure, pathogen pressure, aggression, foraging success, metabolism and sexual selection. Consequently, sociality affects the evolution of a wide range of behavioural, morphological and life history traits" (Reiczigel et al 2008 p715).

The physiology of an animal influences the cohesion of their group, and this is through, for example, similar capacities for movement between group members, neurophysiological characteristics related to information processing of rules and data from the environment (Seebacher and Krause 2017). "Physiological characteristics of individuals can, therefore, influence cohesion of the group, and segregation (fission) and association (fusion) patterns. Determining the link between the physiology of individuals and higher-level interactions is significant, because it may explain dynamics at all group sizes: from groups of few individuals to populations that must respond to environmental variability such as climate change" (Seebacher and Krause 2017 p2).

The "activity synchronisation theory" (Conradt and Roper 2000) proposes that a group remains together only if all members are in the same place at the same time, and this requires a synchronisation of activity (eg:

foraging) by individuals to gain the benefits of group membership (table 4.1). But if two individuals differ in speed of movement, say, one individual experiences a cost if they synchronise their behaviour to the other. For example, Pacific bluefin tuna (Thunnus orientalis) move by active swimming and gliding periods, where the latter uses much less energy, but smaller individuals have to actively swim more to keep up with the gliding larger individuals (and thus use more energy) (Seebacher and Krause 2017).

Seebacher et al (2016) calculated that the slowest zebrafish (Danio rerio) would need to consume an extra 1-2% of its own body mass of food after one hour of moving to keep up with the fastest individual in the group (Seebacher and Krause 2017).

Seebacher and Krause (2017) commented: "As a result, individuals with similar phenotypes may cluster within groups. Alternatively, groups may segregate and fuse into new groups composed of individuals with similar physiological phenotypes... As a consequence, gene flow within populations can be non-random if reproductive events increase with proximity between individuals, and ultimately populations may diverge genetically" (p3).

Advantages

1. Safety from predators.
2. Food; eg: co-operative hunting.
3. Mate access.
4. Communal care.
5. Social transmission of information.
6. Other benefits like thermoregulation.

Disadvantages

1. Increased competition.
2. Increased risk of infection (appendix 4A).
3. Exploitation by other animals.
4. More obvious to predators.
5. Risk of inbreeding.
6. Risk to young; eg: misdirected parental care; infanticide (appendix 4B).

Table 4.1 - Main advantages and disadvantages of group living.

The same behaviour, however, can prove an advantage or a disadvantage depending on the species. For example, in long distance flying, certain birds, like the northern bald ibis (Geronticus eremita) benefit from travelling in the V-shaped echelon as individuals take turns in leading, which is most energetic, and following (Voelkl and Fritz 2017) [19] [20]. Pigeons, on the other hand, gain no energetic advantage from flying together, and may actually have higher costs as "flap frequency increases when flying close behind another bird as a result of aerodynamic interactions" (Seebacher and Krause 2017 pp3-4) [21].

The size of the group will also be a trade-off between advantages and disadvantages. For example, if food availability is low, the competition will be greater in larger groups, and foraging alone may appear more advantageous. On the other hand, groups could become smaller in such situations, though this increases the individual risk of predation. Markham and Gesquiere (2017) described this type of trade-off among pregnant primates with high energy demands.

One strategy, particularly in relation to co-ordination in larger groups, is "by forming several smaller groups with stronger bonds within the one larger group... each individual would maintain complex relationships with a small number of conspecifics, and a larger number of relatively loose relationships that require less information processing" (Seebacher and Krause 2017 p5).

4.2. COMMUNAL NESTING

Animals can congregate close together for specific reasons, like around water bodies in arid areas, or Nile crocodiles at a wildebeest migration river crossing point (Natusch et al 2016).

Natusch et al (2016) studied another example - metallic starlings (Aplonis metallica) (figure 4.1) who nest in large colonies (of hundreds of individuals) in the same trees in Queensland, Australia, to raise their young each year (between November and April). Afterwards, they migrate to New Guinea, but return to the same tree for many years. The researchers used five years of observations of 27 colonies from the Lockerbie Scrub at the northern tip of the Cape York Peninsula.

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[19] The researchers studied fourteen juvenile individuals on a human-led migration (by ultralight aircraft). Members of the group shared leading and following based around dyadic reciprocation (ie: co-operation by pairs of birds) (Voelkl and Fritz 2017).

[20] Forming flocks for migration, even if the birds are usually solitary, also helps in predator protection (Voelkl and Fritz 2017).

[21] Lone larger birds can save energy by soaring-gliding flight, which uses rising air rather than wing flapping (with a saving of up to 95% of energy). But soaring-gliding is slower, and the migration path is limited by the presence of updraughts (Voelkl and Fritz 2017).

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

Figure 4.1 - Metallic starling.

The trees chosen (eg: poison-dart tree, Morton Bay ash) have an abundance of invertebrates (prey), and the carpet of fallen seeds and bird guano beneath attracts them and other animals (eg: pigs, Brush turkeys). Scrub pythons (predators), for example, were also present to capture fallen eggs and birds (figure 4.2).

Natusch et al (2016) summed up: "Each year, breeding colonies of metallic starlings alter the spatial and temporal heterogeneity of wildlife distributions in the rainforests of Cape York. Our surveys documented considerable abundances of soil invertebrates, flying insects, amphibians, reptiles, birds and mammals under bird-nesting trees. There were no similar aggregations under otherwise-similar trees that lacked bird colonies. Moreover, many predators aggregated at colony sites only or primarily at times of year when the birds were nesting. The magnitude of the effect was extraordinary, with densities of many taxa 100 to 1000-fold higher under colony trees than elsewhere" (p9).

The extent of this "ecological hot-spot" is unique because of the variety of species attracted, though similar examples are known, like nesting colonies of silver gulls on small islands supporting many predatory tiger snakes (Natusch et al 2016).

(Source: Natusch et al 2016 figure 1)

Figure 4.2 - Pictures of (a) tree used by starlings, (b) scrub pythons feeding on fallen chicks at night, (c) other birds under the colony tree, and (d) pigs under the tree in the day.

4.2.1. Eusocial Insects

Social insects show intra-colony co-operation and division of labour (DOL), which is defined as "any temporary or permanent behavioural pattern which results in some individuals in the colony performing different functions from the rest" (Brahma et al 2018 p756). Eusocial insects have reproductive DOL (ie: a limited number of individual reproduce and the rest of the colony do not), and non-reproductive individuals performing the tasks of maintaining and defending the nest, and feeding the brood. There is even further DOL, where some individuals forage, for example (extranidal tasks - ie: outside the nest), and others feed the larvae (intranidal tasks - ie: within the nest).

Is this DOL inevitable? This is difficult to study in large colonies, so Brahma et al (2018) performed experiments with small numbers of an eusocial wasp Ropalidia marginata. Female wasps were kept in one of three conditions - solitary (control group), pairs, or triplets.

Half the solitary wasps initiated nest behaviour, which took around 40 days to occur, while two-thirds of the other two groups initiated nests in around fifteen days. The wasps' productivity (ie: number of eggs) was due to DOL [22]. All pairs and triplets (34 and 30 groups respectively) showed reproductive DOL (ie: one individual developed ovaries and laid eggs). Brahma et al (2018) stated that "reproductive DOL is therefore an invariant property of any group of wasps with two or more individuals. In all cases the non-egg layer also participated in building the nest, feeding larvae, and other activities, both intranidal and extranidal. Thus, cooperation is also an invariant property of any group of wasps with two or more individuals" (p759).

4.3. ALLOPARENTAL CARE

Within a group, alloparental care can take place. This is "any non-parent taking part in the process of raising young, by engaging in behaviours that benefit the young" (Augusto et al 2017 p440). There are two types (Kleiman and Malcolm 1981). "In direct parental care there is an interaction with the young, such as grooming, huddling, or providing food, which can increase the probability of survival of the young. When the behaviour is not directed towards the young, but still influences its survival, it is considered indirect alloparental care, for example shelter construction and maintenance, or sentinel behaviour" (Augusto et al 2017 p441).

Babysitting is an example of direct alloparental care as seen in meerkats, where the babysitters can lose up to 2% of body weight per day for this duty (Clutton-Brock et al 2001).

Augusto et al (2017) studied the long-finned pilot whale (Globicephala melas) off Cape Breton Island, Nova

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[22] "Mating is not essential for a female wasp to build a nest, develop her ovaries, lay unfertilised eggs, and even become the sole egg layer of a colony despite the presence of other mated individuals..." (Brahma et al 2018 p757).

Scotia, Canada, between 2009 and 2011. Using DNA samples and visual identification, it was calculated that around three-quarters of calves had alloparents (ie: adults escorting calves).

The researchers admitted key methodological limitations with their study:

- Visual identification of individuals by dorsal fin marks. These marks can be "gained by injuries..., interacting with other individuals, predators, boats, or fishing gear. Pilot whale calves are born with unmarked or with very small marks on their fins. This means that for most calves we have to use other, more temporary, markers to identify individuals. Marks can be found on both dorsal fin and body..., but are usually restricted to one side of the individual. This makes it harder to identify both sides of a calf, and to identify it over several years" (Augusto et al 2017 p448).

- Alloparental care was categorised only after two separate observations. "The study population is in the thousands. Data are collected from an opportunistic vessel, giving limited encounter durations. Also, groups are not often seen repeatedly on different trips on the same day. Likewise, the photographic data are difficult to collect for both calf and companion simultaneously" (Augusto et al 2017 pp449-450).

The social spider Stegodyphus dumicola (colonial spiders) lives in nests where only a few females mate and males die early leaving many unmated females [23]. Mothers show extreme and suicidal maternal care, including guarding eggsacs, regurgitated feeding of the hatched spiderlings, and matriphagy (where the offspring consume the mother) (Junghanns et al 2017). Do the unmated females provide allomaternal care?

Junghanns et al (2017) investigated this question with a study of spiders from 24 nests in South Africa. The researchers created 192 groups of two mated females and three virgin females. Allomaternal behaviour was observed in a number of groups, including matriphagy of virgins, and virgins were more likely to attack prey than mother, which "requires abandoning the safe retreat, attack of a potentially dangerous and defensive prey" (Junghanns et al 2017 p105). This is evidence of co-operative breeding.

In nests, a large proportion of females remain unmated, and through allomaternal care "these virgin females gain considerable inclusive fitness benefits

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[23] This is scramble competition as males mature early and mate with first adult females available.

because of the high genetic relatedness among individuals in the nest" (Junghanns et al 2017 p105).

4.4. RESCUE BEHAVIOUR

Rescue behaviour has been observed in ants in response to predator threat, and injured nestmates. In the former case, nestmates who fall into an antlion trap are pulled out or the antlion attacked (eg: Nowbahari et al 2009).

In the example of injury, Matabele ants (Megaponera analis) carry injured ants back to the nest after raiding termites.

Frank et al (2017) observed this behaviour in northern Ivory Coast in 2013. Four hundred and twenty raids on termite nests were observed, and for 54 raids, the injured ants being carried back were counted and examined. Subsequently, in laboratory colonies, injuries were experimentally manipulated (eg: cutting off one leg with scissors).

The majority of the ants carried back to the nest were seen in later raids. The rescue behaviour thus appears profitable, particularly as injuries are rarely fatal. In the experiments, injured ants were not picked up if found on the outward journey to raid termites. "It seems unlikely for the ants to ever encounter this situation naturally" (Frank et al 2017 p4).

Frank et al (2017) concluded that "rescue behaviour, focused specifically on injured and handicapped individuals after hunting, is unique in social insects" (p5). They outlined the reasons for its evolution in these ants:

- Group-hunting species.

- Raiding is a separate behaviour to foraging generally (ie: the ants march outward together and wait after the fight to return together).

- Most injuries are non-lethal.

- The benefits of rescue for the colony outweigh the costs (eg: carrying back injured nestmate not at the expense of not carrying back prey).

- Each individual is valuable to the colony (ie: relatively low population turnover).

4.5. CO-OPERATION

Plotnik et al (2011) showed co-operation in experiments with twelve elephants at a conservation centre in Thailand. Two bowls of food were placed on a sliding table that could be reached if two elephants together pulled separate ropes to bring the table towards them. There were three conditions:

i) Two elephants together (simultaneous release condition) - On over 80% of trials the pair pulled together.

ii) One elephant waited for up to 45 seconds until another elephant arrived (delayed release condition) - The first elephant waited for a partner on over 90% of trials.

Seed et al (2008), for example, reported in similar experiments that rooks co-operated in a simultaneous release condition, but "failed to wait for each other in the delayed release condition" (Plotnik et al 2011).

iii) One end of the rope was not connected to the table when two elephants arrived together (no-rope control condition) - Almost all the elephants understood the need for a partner.

Studies with other species, like hyenas (Drea and Carter 2009), found that the animals "learned the need for a partner, but it was unclear whether they understood their partners' behavioural contribution. Chimpanzees, on the other hand, have demonstrated clear knowledge of both a partner's role and contribution" (Plotnik et al 2011 p5120).

Plotnik et al (2011) concluded: "Our own study shows that elephants not only (i) co-operate successfully in a coordinated pulling task but also (ii) recognise the need for a partner by waiting if the partner is delayed. Elephants perhaps also (iii) recognise the necessity of their partner's actions, given that they discriminate between a partner with or without rope access. As with humans and other primates, it is hard to draw a line between learning and understanding, however. The least we can conclude is that the elephants demonstrated co-operative behaviour in this experiment with attention to their partner's presence and actions, thus showing a well-developed propensity toward partner-oriented, deliberate co-operation" (p5120).

4.5.1. Trading Favours

Reciprocal co-operation" among humans means "paying like with like", whereas, with "reciprocal trading", the "exchanges between social partners may involve different commodities and services" (Schweinfurth and Taborsky 2018 p594).

Schweinfurth and Taborsky (2018) showed the latter among Norway rats (Rattus norvegicus) exchanging food provisioning for allogrooming and vice versa. It was already known that rats exchange food for food, and grooming for grooming.

The researchers tested 37 pairs of adult female rats in four different situations. One rat of the pair was the forced rat, and they experienced co-operation or non-co-operation by their partner with food or allogrooming. This was the "experience phase". The focal rat later had the opportunity to return the favour (table 4.2).

In the "test phase", the focal rat could return the favour with a different "commodity". "Focal rats groomed previously co-operative food providers more often than non-co-operative ones..., and focal rats provided more food to previously co-operating high groomers than to low groomers..." (Schweinfurth and Taborsky 2018 p595).

Condition	Experience phase	Test phase
1	Received grooming from co-operative partner	Opportunity to provide food to partner
2	No grooming received (non-co-operative partner)	Opportunity to provide food to partner
3	Received food from co-operative partner	Opportunity to provide grooming to partner
4	No food received (non-co-operative partner)	Opportunity to provide grooming to partner

(Based on Schweinfurth and Taborsky 2018 figure 2)

Table 4.2 - Four conditions of experiment.

Exchanging different "commodities" has been described as "ultra-social" behaviour (Tomasello 2014), and is most common in humans. However, it has been reported in other primates. For example, vervet monkeys provided allogrooming for getting access to food in a field experiment (Fruteau et al 2009), and chimpanzees in the wild have been observed to trade meat for sex, for instance (Gomes and Boesch 2011).

4.5.2. Co-operation or Not

Humans, even from 1 year old, prefer individuals who have been seen to be helpful to others rather than unhelpful, but Krupenye and Hare (2018) showed the opposite in bonobos in four experiments.

In the first experiment, 24 bonobos [24] saw an animation of a shape being helped or hindered by another shape to climb a hill. All participants showed a significant preference for the unhelpful shape.

In the second experiment, 22 bonobos saw eight demonstrations where a neutral actor dropped a toy out of reach, and a helping adult returned it while a hindering adult tried to stop this action. The bonobos' preference was measured by both the helping and hindering adult offering a piece of apple simultaneously. Food was taken from the latter more often.

Experiment 3 was a replication of this previous one with a baseline measurement of the bonobos' preference for an adult. The preferred adult subsequently became the helper when the toy was dropped. All eighteen bonobos still took food from the hinderer. "Taken together, these three experiments demonstrate that bonobos have a robust preference for individuals that behave anti-socially over those that behave pro-socially toward others" (Krupenye and Hare 2018 p283).

Krupenye and Hare (2018) believed that these findings could be explained by the "dominance hypothesis" - ie: the hinder is perceived as a dominant individual, and "dominant individuals may be the most desirable allies or social partners". Krupenye and Hare (2018) continued: "Although in principle pro-social and anti-social individuals can be dominant or subordinate, anti-social behaviour is often used to establish and maintain dominance..." (p283).

This was tested in Experiment 4 where the animation from Experiment 1 was adapted to signal dominant or subordinate shapes. Twenty-four bonobos participated and significantly preferred the "dominant" shape.

However, the preference of humans for moral over immoral character traits in others can be context-dependent, as shown recently by four experiments by Melnikoff and Bailey (2018) [25].

Experiment 1 - Participants met two "individuals" (coloured avatars), who were presented as merciful or merciless, where either trait was relevant (goal-conduciveness). The participants were involved in fictional criminal cases as defence lawyers (where mercy is valued) or prosecuting lawyers (where mercilessness is valued).

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[24] In total, 43 semi-free-ranging adult females were tested at a sanctuary in the Democratic Republic of Congo.

[25] The "morality dominance hypothesis" noted that "positive morality traits are always positive in person perception, and negative morality traits are always negative" (Landy et al 2016 quoted in Melnikoff and Bailey 2018).

Participants playing defence lawyers showed a preference (96% of the time) for "individuals" described as merciful, and prosecuting lawyers for merciless (94% of the time).

Experiment 2 - In a fictional spy game, participants met "individuals" who were honest/trustworthy or dishonest/untrustworthy. Participants played agent "Mu", described as honest, or agent "Eta", described as dishonest. Participants preferred the "individual" who was similar to their spy character to help achieve their goal.

Experiment 3 - Participants who were involved in committed romantic relationships or not were presented with a women who showed fidelity or infidelity. It was predicted that participants in committed relationships would prefer the woman showing fidelity, and single participants the other one. This was found for male participants only.

Experiment 4 - Participants played an economic game involving sharing money. They were arbitrarily labelled as "fair" or "unfair" players before meeting an altruistic or a non-altruistic player. It was expected that "fair" players would prefer altruistic players and "unfair" players non-altruistic partners. This was found to be so.

Melnikoff and Bailey (2018) concluded that "the results of four studies suggest that the valence of morality traits in others is conditional. Specifically, the preference for morality vs immorality in others can be eliminated or reversed when one's current goals are best served by an immoral person" (pE599).

4.6. SOCIAL SUPPORT

Stress can be reduced by social buffering, "in which social support provided by bond partners cushions the aversive effects of stressful events through mediation of the hypothalamic-pituitary-adrenocortical (HPA) axis" (Wittig et al 2016 p2). "Bond partners" also make social interactions more predictable with less conflict.

Wittig et al (2016) investigated these ideas with over two years of observations of chimpanzees in Uganda. Urine samples were used to measure stress via levels of urinary glucocorticoids (uGC) [26]. Bond partners were categorised based on co-operative behaviours like

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[26] Higher levels mean greater stress response.

grooming and food sharing, and low levels of aggression. Stress was created by the researchers making drumming sounds to simulate the nearby presence of rival groups of chimpanzees.

It was found that "relative urinary glucocorticoid levels were lower when engaging with bond partners rather than other individuals, whether during a stressor (intergroup encounters), everyday affiliation (grooming) or resting" (Wittig et al 2016 p3). The presence of a bond partner reduced uGC levels most during stressful events. For example, the difference in relative uGC levels was about one-third in stressful situations with the presence or absence of a bond partner, but there was little difference in uGC levels in a resting situation with or without a bond partner.

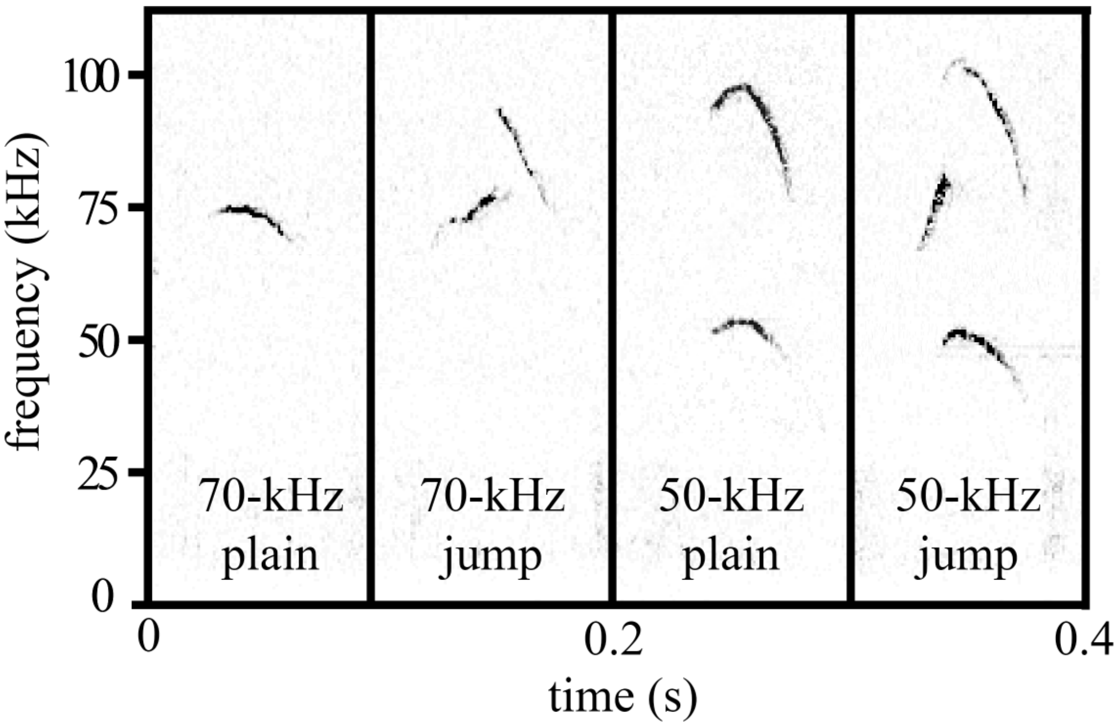
4.7. EARLY LIFE SOCIAL DEPRIVATION

An adult animal's "social competence" is its "ability to fine-tune its behaviours during social interaction either across or within social contexts" (Keesom et al 2017 p1). Individuals raised in "socially impoverished environments" (eg: isolation) have poorer social competence. For example, overexpression of aggression (appendix 4C), including displays of aggression at inappropriate times, and poorer courtship and mating behaviour (eg: lack of preference between mates of differing quality) (Keesom et al 2017). Kempes et al (2008), for example, reported that female rhesus monkeys, who were socially deprived, showed more aggression towards a stranger rhesus attempting to groom them (an affiliative behaviour) than non-socially deprived individuals.

House mice (Mus musculus) have been studied extensively here. For example, Chabout et al (2012) showed differences in ultrasonic vocalisations (USVs) (used in social signalling) during encounters with males between group-housed and individual-housed adult males.

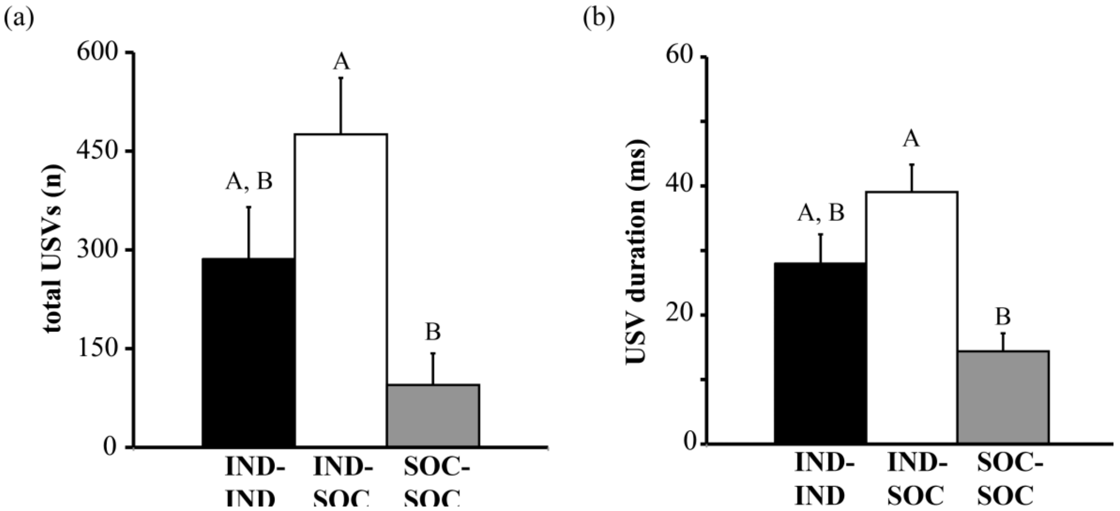
Keesom et al (2017) explored this further by housing 36 three-week old males alone or in social groups of four males together for five weeks. Then two unfamiliar males were placed together to study their social interaction, either two individually housed mice (IND-IND), two socially housed (SOC-SOC), or one of each (IND-SOC). The behaviour was filmed and the USVs recorded for analysis by spectrograms (figure 4.3).

There were significant differences in the total USVs and their duration between conditions. The most and longest were found in the IND-SOC condition (figure 4.4). There were also differences in the type of USVs (figure 4.5). Differences were observed in non-verbal behaviours



(Source: Keesom et al 2017 figure 1)

Figure 4.3 - Four USVs produced by mice during same-sex encounters.

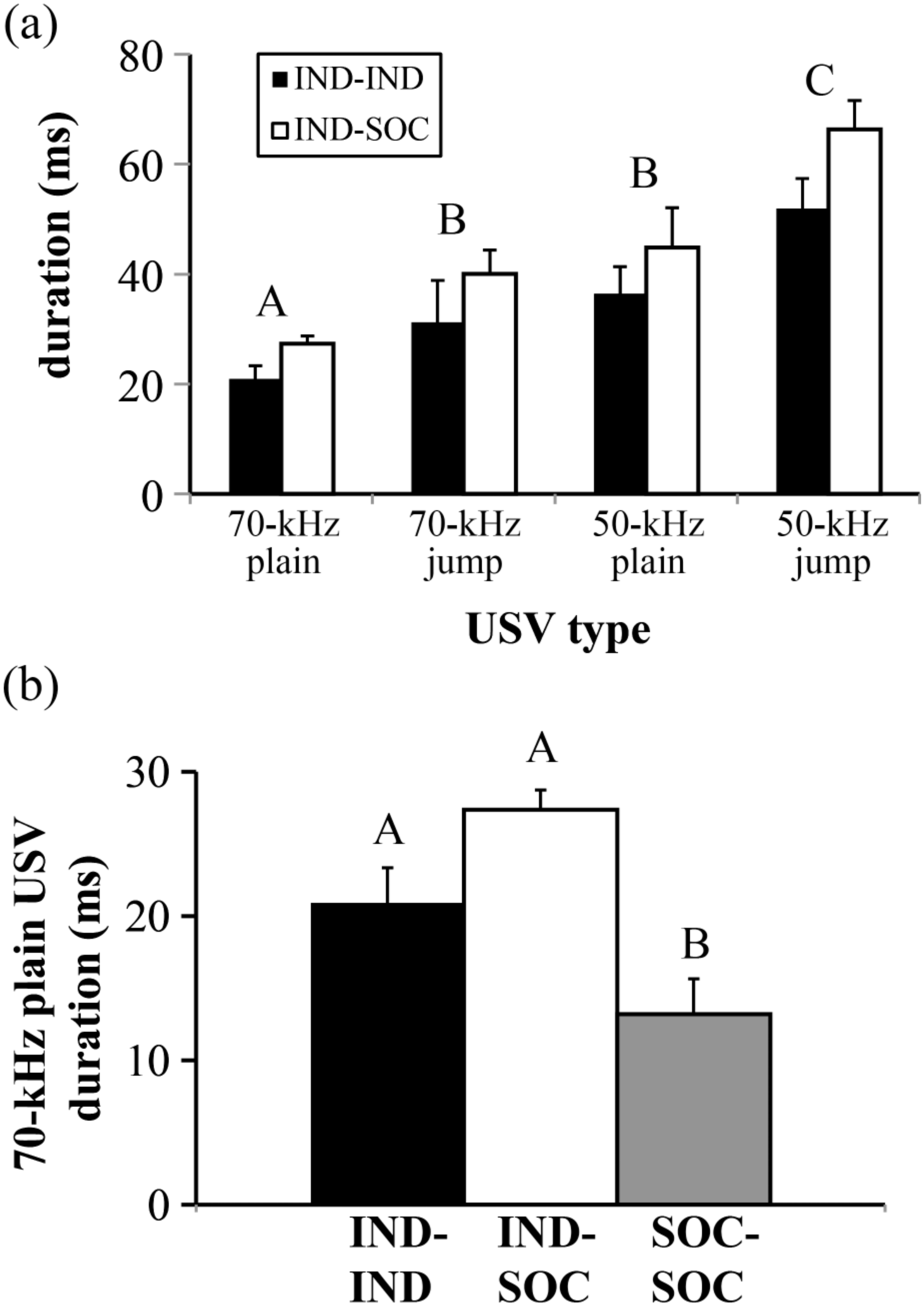


(Different letters = significantly different)

(Source: Keesom et al 2017 figure 2)

Figure 4.4 - Total number of USVs (a) and duration (b) based on condition.

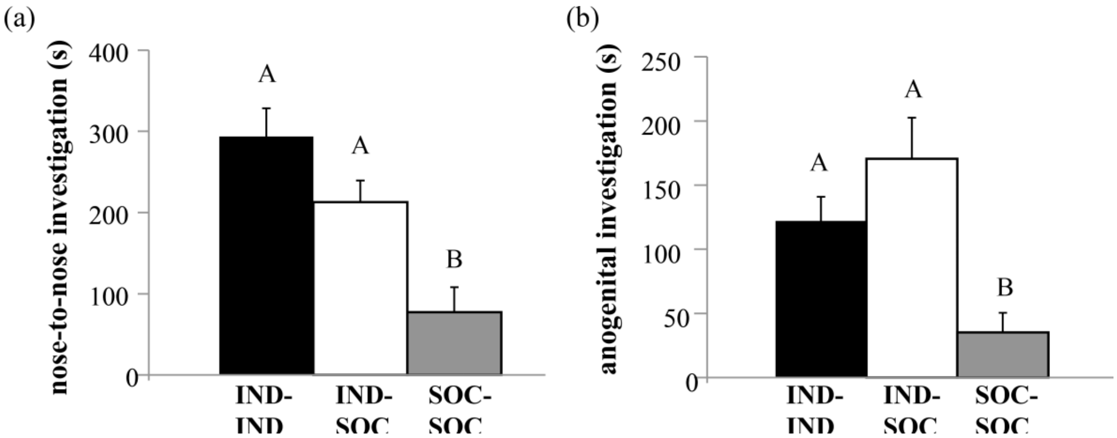
(eg: more social investigation by individually-housed mice) (figure 4.6).



(Different letters = significantly different)

(Source: Keesom et al 2017 figure 4)

Figure 4.5 - Mean duration of specific USVs (a) and "plain" USV (b) based on condition.



(Different letters = significantly different)

(Source: Keesom et al 2017 figure 5)

Figure 4.6 - Social behaviours - nose-to-nose investigation (a) and anogenital investigation (b) - based on condition.

Overall, more USVs were emitted in IND conditions than the SOC-SOC one, and individually-housed mice exhibited increased mounting behaviour towards socially-housed mice. The researchers felt that this behaviour was not inappropriate courtship and mating behaviour, but an inability to distinguish between aggressive and non-aggressive individuals by the individually-housed mice (as same-sex mounting is used to establish dominance). So, "socially incompetent individuals do not grade their behaviour in a way appropriate to a given situation" (Keesom et al 2017 p12). The researchers continued: "The idea that social experience allows animals to appropriately grade aggressive behaviour is supported across taxa. For example, animals that have gained social experience via group-living employ strategies other than actual fighting, such as aggressive or submissive signals, when encountering new individuals... In contrast, animals that are raised in an impoverished social environment, as opposed to being raised in larger or more complex groups, typically rely solely on physical aggression, and are therefore less able to interact peacefully with new conspecifics, a phenomenon that is demonstrated in fish, birds, rodents, and primates" (Keesom et al 2017 p13).

Both verbal and non-verbal behaviours were shown to be affected by early social experience in this research.

4.8. APPENDIX 4A - INFECTION SPREAD

One major drawback of group living is the rapid spread of disease. Consequently, social animals have evolved strategies to deal with this risk, like swift recognition of physical appearance, behaviour, and chemical odour changes of sick group members (eg: tadpoles, mice, lobsters) (Pull et al 2018). In response to this recognition, interactions with the sick individual are reduced or avoided completely. Healthy individuals may also have a boost in their immune system in preparation.

So, there is an advantage for sick individuals to hide their illness to avoid shunning, unless kin will be infected, or signs of sickness elicit care (Pull et al 2018).

Social insects, like termites and ants, have both these factors. So, "an animal that warns its relatives if it is sick is likely to have a greater inclusive fitness than an animal that does not, since fewer of its kin will fall sick and suffer reductions in fitness... Hence, in closely related social groups, there may be selection for both the detection of illnesses by healthy group members... and the advertisement of an animal's disease status by sick individuals themselves" (Pull et al 2018 p2).

Like a "superorganism", ant colonies appear to have evolved collective disease defence (or "social immunity"). For example, Pull et al (2018) found that the invasive garden ant (Lasius neglectus) has evolved a "destructive disinfectant", which is sprayed on pupae infected by a fungal infection killing both the pupae and the infection.

4.9. APPENDIX 4B - INFANTICIDE

Infanticide, where males kill unrelated infants, is sometimes used to induce the mother to become sexually receptive immediately (sexual coercion hypothesis) [27]. It has been observed in many primate species (Nishie and Nakamura 2018).

Infanticide is not unknown in wild chimpanzees, but Nishie and Nakamura (2018) observed the rare case of infanticide immediately after birth at Mahale Mountains National Park. Observed delivery in the wild is uncommon as mothers perform "maternity leave" (Nishida et al 1990) (ie: hide away alone to give birth) as a counter-strategy to infanticide.

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[27] Other reasons include to eat the meat (ie: cannibalism) (nutritional benefit hypothesis) or to remove future competitors (resource competition hypothesis) (Nishie and Nakamura 2018).

4.10. APPENDIX 4C - GAPING DISPLAY

An aggressive display found in many animals is the "gaping display", where "an open mouth is presented toward an intruder for territorial defence... to advertise body size, the size of a weapon (jaws and teeth), or a structure that infers a weapon's performance" (Hongjamrassilp et al 2018 p626). For example, mandrills gape to show their large teeth, and male collared lizards reveal mouth muscles that signal bite force (Hongjamrassilp et al 2018).

Gaping is also common in fishes like the Sarcastic Fringhead (Neoclinus blanchardi) (figure 4.7), which shows exceptional gaping behaviour. The male of this fish seeks holes on the sea floor for refuge from predators and as egg-deposition sites for females, so male-male competition is fierce. The gaping shows the opponent both the teeth, and the thick adductor mandibulae muscles, which is an honest signal of biting performance (Hongjamrassilp et al 2018).

(Source: James Martin; in public domain)

Figure 4.7 - Dead Sarcastic Fringehead showing large gaping ability.

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5. CLEVER ANIMALS

5.1. COCKATOO DRUMMING

Male palm cockatoos (Probosciger aterrimus) (figure 5.1) in northern Australia have been observed to produce a rhythmic drumming, during their vocal and visual displays, by striking a hollow tree trunk with a stick. The drumming occurs alongside calling and crest erection, for instance, but also by itself. "This behaviour is remarkable because tool manufacture among non-human species is rare and almost always occurs in the context of solving problems related to foraging, but palm cockatoos use their tools only to make sounds" (Heinsohn et al 2017 p1).

Drumming or percussion using body parts, like hands, feet or beaks have been reported in other species (appendix 5A) (eg: Java sparrow; Soma and Mori 2015; appendix 5B).

Heinsohn et al (2017) observed eighteen males and made 131 recordings between 2009 and 2015 in Kutini-Payamu (Iron Range) National Park, Cape York Peninsula, Northern Australia. A drumming sequence was defined as "continuous drumming with less than five seconds between taps" (p4). Most drumming occurred in the presence of a female. Thus, suggesting that "drumming is predominantly performed in inter-sexual displays" (Heinsohn et al 2017 p2). Furthermore, the nests of neighbours are too far away to hear it.

(Source: Stavenn)

Figure 5.1 - Palm cockatoo.

Two types of sound tools were noted. Firstly, drumstick making, where branches of an appropriate length (around 20 cm) are broken off, and the foliage removed. This appears to be a variation of the behaviour of breaking off branches to use as a nesting platform in hollows of trees. Secondly, the hard seedpod from Grevillea glauca (bushman's clothes peg or beefwood tree) is shaped.

Palm cockatoos also inhabit lowland Guinea, and reports of drumming using the clenched foot have been made, but not tool use (Heinsohn et al 2017).

Heinsohn et al (2017) concluded: "Palm cockatoos suggest an evolutionary link between regular rhythm and solo-based percussive performances by males to females. This supports Darwin's [1871] contention that a regular beat has primeval aesthetic appeal across species, and points to the distinct possibility that the preference for a regular beat in human societies had other origins before being co-opted into group-based music and dance" (p3).

5.2. TOOL USE

The Goffin's cockatoo (Cacatua goffiniana) (figure 5.2) makes stick-type tools [28]. This was first noticed by Auersperg et al (2012) when a captive individual ("Figaro") "spontaneously and reliably manufactured tools by cutting splinters out of larch wood, using them to rake in food placed behind the aviary grid" (Auersperg et al 2016 p1).

(Source: Joseph Smit, Proceedings of the Zoological Society of London 1875; in public domain)

Figure 5.2 - Drawing of Goffin's cockatoo.

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[28] Tool use has been reported in a variety of other species (appendix 5C).

Auersperg et al (2014) subsequently found that three other males could copy this behaviour after tool use (not manufacture) demonstrations. This study also used larch wood, and Auersperg et al (2016) noted that because "the material breaks more easily along the age lines of the tree, it was unclear whether the elongated shape of the tools they made was accidental. Although the tools were of sufficient length and shape (ie: slim enough to fit through the grid and long enough to reach the target) the animals might, for example, have bitten and torn the material out at random places, accidentally producing splinters that served as elongated, functional tools" (pp1-2).

These researchers tested these three males and "Figaro" with a specially designed puzzle. A nut was placed out of beak or claw reach in a plastic box, but it could be pulled out with a short stick. Four different substances were presented, which could be shaped into an appropriate stick. All the birds were successful using a variety of substances (larch wood, beach twig, and cardboard, but not beeswax).

Auersperg et al (2016) observed: "Goffin's cockatoos do not build nests, nor are they known to be specialised for using foraging tools in the wild... This suggests that tool related behaviours in this species are unlikely to express heritable predispositions for tool use, tool making or nest building as is the case in some corvids. Their tool-related competence in the laboratory offers a valuable opportunity to isolate events of individual innovation" (p1).

5.2.1. Inherited Ability?

Rutz et al (2016) studied 104 of the surviving 109 Hawaiian crows or Alala (Corvus hawaiiensis) (figure 5.3), which is extinct in the wild in the 21st century (ie: only exists in captivity at two conservation centres in Hawaii and at the San Diego Zoo Safari Park in 2013; Rutz et al 2016). Around four-fifths of the birds were found to spontaneously use tools to access out-of-reach food.

A log with specially drilled holes was baited with food, and twelve sticks of different length were left nearby. The food could only be accessed by use of a stick (tool).

The fact that the majority of a whole species showed tool use suggests that the behaviour has a genetic basis (which has been proposed for the sophisticated tool use-using New Caledonian crow (Corvus moneduloides) (Kenward et al 2006).

To test this idea, Rutz et al (2016) reared seven juvenile Alala without an opportunity to observe adults using tools. Five of these individuals were successful in

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

Figure 5.3 - Hawaiian crow or Alala.

gaining food with a stick. Rutz et al (2016) concluded that while the "rearing experiment demonstrated conclusively that naive Alala can independently develop functional tool use, environmental conditions are likely to affect behavioural development" (p403).

The evolutionary basis to tool use comes from "a propensity to 'discover' tool-assisted foraging solutions independently, which probably results from genetically canalised, persistent object-exploration behaviour" (Rutz et al 2016 p404).

In relation to the New Caledonian crow, the Alala is "only distantly related, suggesting that tool-related adaptations evolved convergently" (Rutz et al 2016 p405).

5.3. RATS AND METAMEMORY

Metamemory is knowing whether an individual remembers something. It is an ability routinely shown by humans, but difficult to test in non-humans. One method is to give the animal the opportunity to decline tests, and rhesus monkeys, for example, showed this behaviour (Hampton 2001). "Monkeys were more accurate on trials they chose to take than they were on other trials that were presented in which there was no option to decline the memory test. A performance advantage on chosen trials as compared to forced trials results from adaptively declining difficult tests and indicates metacognitive responding" (Templar et al 2017 p892).

Templar et al (2017) tested nine male rats. The delayed match to sample (DMTS) memory test was used. A rat was presented with a particular scent, and then, after a delay, four cups where one had the matched scent and contained food. The delay was up to thirty seconds.

Metamemory was tested by giving the rats the opportunity to decline DMTS test on two-thirds of trials and not on the other trials. "Performance was significantly higher on chosen trials than on forced trials..., indicating that rats adaptively used the decline option on chosen trials when memory was weak" (Templar et al 2017 p897). The rats were more likely to decline trials with long delays than short ones.

5.4. PLANNING

Planning involves thinking beyond the "current sensory context", and it requires "a host of cognitive skills, including mental representation of a temporally distant event, the ability to outcompete current sensorial input in favour of an unobservable goal, and understanding which current actions lead to the achievement of the delayed goal" (Kabadayi and Osvath 2017 p202). Great apes, for example, have been found to show planning in experimental situations (Kabadayi and Osvath 2017).

Corvids have also shown it. "It is unlikely that such advanced skills were present in the last common ancestor of birds and mammals (320 million years ago) and instead must have evolved independently. This vast phylogenetic separation has provoked scepticism concerning whether corvid planning really is functionally similar to that of hominids. It has been contended that the — admittedly flexible — skills of corvids, which are habitual food cachers, may instead reflect adaptations confined to the food-caching domain" (Kabadayi and Osvath 2017 p202).

Kabadayi and Osvath (2017) showed planning in experimental situations with behaviour unfamiliar to ravens (Corvus corex) - ie: tool use, and bartering. Four experiments were performed with five birds:

Experiment 1 - This tested planning for fifteen minutes into the future. After training, the birds were given a choice of objects (of which a stone would act as a tool or a token to exchange for food) to use 15 minutes later. In the tool version, the tool was chosen and used to gain food in 80% of trials, and tokens (in the social bartering version) were chosen correctly on 92% of trials.

Experiment 2 - The same experiment as above, but the time interval was 17 hours (overnight). The correct item was chosen in around 90% of trials.

Experiment 3 - This experiment tested planning as delayed gratification (self control). Similar to the previous experiment, but the birds were faced with an immediate small food reward as a choice or choosing an object to use 15 minutes later for a larger food reward. The tool and token were chosen on 73% of trials.

Experiment 4 - In this experiment, the immediate small food reward was placed closer than the objects to choose from for use 15 minutes later. In all trials the birds ignored the nearby food.

Kabadayi and Osvath (2017) summed up their findings: "This study suggests that ravens make decisions for futures outside their current sensory contexts, and that they are domain-general planners on par with apes. In the tool conditions, including self-control, the ravens were at least as proficient as tool-using apes. In the bartering conditions, the ravens outperformed orang utans, bonobos, and particularly chimpanzees" (p203).

5.5. TIMING

A well-developed sense of time (ie: the ability to perceive a certain period of time passing) can be important to animals in foraging or navigation. It has been studied in a selection of species (eg: bumble bees; goldfish; rats; pigeons; cats; appendix 5D) (Heinrich et al 2016).

Heinrich et al (2016) studied a male harbour seal (Phoca vitulina) (figure 5.4) in an experimental chamber in Germany. The seal was shown an image on a computer screen for 3, 5, 7, 12, 18 or 30 seconds, and then another image for either the same or different length of time. The seal was taught to move its head to the left if the time intervals were the same, or to the right if different. Each session involved thirty trials with equal numbers of same or different intervals.

The seal was able to accurately discriminate between time intervals, and was better where the difference in time interval was larger. This behaviour would be useful in relation to diving for food as this seal is air breathing, and "foraging decisions require an estimation of variables such as energy gain per time, swimming speed, travel duration and bottom, descent and ascent duration. As some dives of the shallow diving harbour seals are characterised by phases lasting seconds to minutes..., interval timing might be required in particular to assist foraging decisions" (Heinrich et al 2016 p1134).

This study involved one individual who was highly trained and so used to artificial experimental situations.

(Source: Maximilian Narr)

Figure 5.4 - Harbour seal.

5.6. UNDERSTANDING FALSE BELIEFS

"Theory of mind" (ie: understanding the beliefs and intentions of others) is common in humans, but less so in great apes. For example, they can distinguish between intentional and accidental actions, and they can perceive what others can or cannot see (eg: subordinates take food that a dominant individual cannot see) (Buttelmann et al 2017).

"But a key marker of advanced social cognition is an understanding of others' false beliefs" (Buttelmann et al 2017 p1). This is the ability of the viewer who knows certain information, but the actor does not, to understand that the actor will act on their beliefs. For example, individual A sees an object placed in box 1 and then leaves the room. Individual B watches the object moved to box 2. Where will individual A look for the object on their return? If individual B understands false beliefs, they expect that individual A will look in box 1.

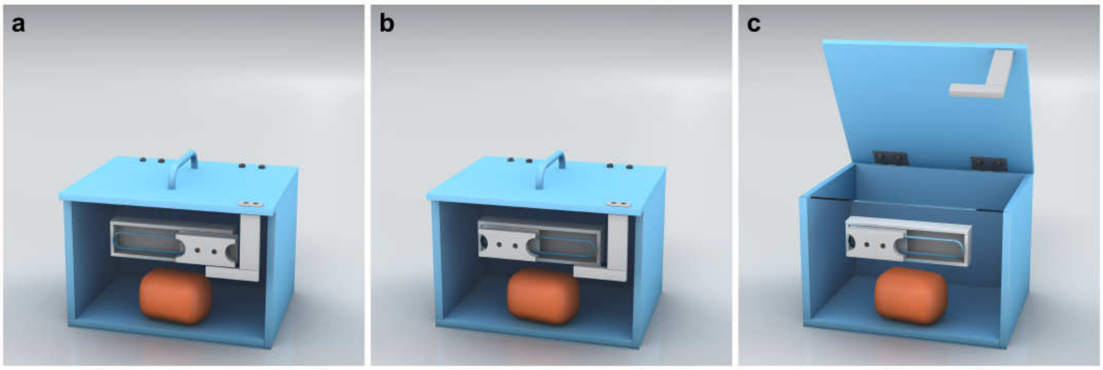
Testing this ability in great apes in experiments is not easy, and many studies find negative evidence (Buttelmann et al 2017). For example, where the ape looks in the violation-of-expectation paradigm (Onishi and Baillargeon 2005) is one method. Using the scenario described above, will the ape look at where the object actually is or the place where the returning individual thinks it is? But if the returning individual goes to the actual place, how does the viewer behaviour (ie: when their expectations of false beliefs are violated)?

Using a similar design, Krupenye et al (2016) found that chimpanzees, bonobos and orang-utans, and two year-old humans "anticipated the location where an actor would search for an object based on the actor's false belief about the object's location" (Buttelmann et al 2017 p2). But Buttelmann et al (2017) are critical of this study: "apes could have passed the test simply by predicting that the actor would go to the last place he saw the object" (p2).

So, Buttelmann et al (2017) used a different design (based on Buttelman et al 2009 with 16-18 month-old human infants). Rather than looking being the measure of false-belief understanding, it was helping behaviour.

Study 1 involved 23 chimpanzees, five bonobos, and six orang-utans at Leipzig Zoo in Germany. In the false-belief condition, the participants observed the experimenter put a toy in the yellow box and leave the room, then the assistant moved the toy to the blue box (and locked both boxes). The experimenter returns and tries to open the yellow box unsuccessfully, while the participant could help (figure 5.5). If the participant has false-belief understanding, they will reach out the object in the blue box for the experimenter. In the true-belief condition, the experimenter is present when they toy is moved (figure 5.6).

The apes helped open the box containing the toy significantly more often in the false-belief than the true-belief condition. This appeared to suggest that that the apes had false-belief understanding. But Buttelmann et al (2017) offered a cautious alternative



(Source: Buttelmann et al 2017 figure S1)

Figure 5.5 - The locked box used in the experiments with the open side accessible to the apes only.

(Source: Buttelmann et al 2017 figure 1)

Figure 5.6 - Set-up in Study 1 where experimenter looks in box based on false belief.

interpretation: "That is, in the false-belief condition, rather than understanding that the experimenter had a false belief about the current location of the object, apes might have understood that he was ignorant about the current location of the object and responded based on a rule such as 'whenever someone is ignorant about where his object is, he will be looking for it'. Although these two different levels of understanding (false belief versus ignorance) would result in exactly the same response behaviour in the current task, the underlying cognitive representations would be different" (p7).

Study 2 replaced the true-belief condition with the ignorance control condition, where the experimenter has no knowledge of where the object is and simply tries to open one of the boxes. Twenty-nine of the apes from the previous study were tested here. Participants behaved significantly differently between the false-belief and the ignorance conditions. This suggested that "they used an understanding of the experimenter's false belief, rather than a simpler rule based on his ignorance, to decide how to help him in the false-belief conditions of these studies" (Buttelmann et al 2017 p8).

Buttelmann et al (2017) believed that the two studies were evidence of a "basic understanding of others' false beliefs".

However, in the true-belief condition in Study 1, half the apes helped open the empty box. "When the experimenter tugged on the box that he knew to be empty, to adult humans... the most natural inference is that he must want to open the empty box for some reason - he cannot want the toy because he knows where it is and he is not trying to open that box" (Buttelmann et al 2017 p9). But why did some apes open the box containing the toy? Buttelmann et al (2017) suggested that the participants had inferred the experimenter's goal in the condition, "it is just that half of them inferred that the goal was to open the empty box and half, for some reason, inferred that it was to get the object" (Buttelmann et al 2017 p9). Buttelmann et al (2009) found similar results in the true-belief condition with human infants.

Buttelmann et al (2017) wondered about their findings compared to the negative results in direction of looking experiments. They suggested that "here participants were required to infer the human's goal and help him achieve it. Reading others' goals is something that apes are quite skilful at in other contexts" (Buttelmann et al 2017 p10).

Note that this study involved captive individuals (probably from birth), and it did include some prior training in relation to the opening of empty boxes.

5.7. CUCKOOS: TWO RECENT STUDIES

5.7.1. Acoustic Mimicry

Acoustic mimicry to produce dishonest signals is seen in less dangerous prey producing the sounds of more dangerous animals (eg: young burrowing owls make a call similar to the sound of a rattlesnake vibrating its rattle; Rowe et al 1986), or in a less dangerous predator mimicking a more dangerous animal. An example of the latter is the rufous-vented ground-cuckoo (Neomorphus geoffroyi) mimicking the teeth clacking of the white-lipped peccary (Tayassu peccari) (hog-like animal) as they "bulldoze the forest floor, rooting through soil, clearing and stirring the forest floor detritus" (Raposo do Amaral et al 2017). This sound causes small vertebrates hidden in leaf litter, say, to flee and the ground-cuckoo can capture them.

5.7.2. Female Cuckoo Calls as Misdirection

The cuckoo (Cuculus canorus) is an example of an obligate brood parasite as the females lay eggs in the nests of other species (eg: reed warbler) (the host), who is tricked into raising the parasite offspring as their own. Thus, the cost of raising the offspring is borne by the host. So there is an incentive for the host to avoid such parasitism.

This has led to an "evolutionary arms race" between host and parasite. For example, hosts reject eggs from the nest that look different to their own, and so cuckoos evolved host egg mimicry. Hosts monitor local cuckoos and mob than near the nest, and cuckoos evolved "remarkable secrecy and speed when they parasitise a host nest" (York and Davies 2017).

York and Davies (2017) observed: "Therefore, it seems paradoxical that female cuckoos often call while they monitor host nests, and especially just after parasitising a clutch" (p1520). The "chuckle" or "bubble" call is similar in frequency and rate to a hawk's call (host predator). York and Davies (2017) argued that the call "tricks the hosts into responding vigilantly as if they were exposed to danger from a hawk, instead of from a cuckoo. This would divert host attention from clutch protection to self-protection, and so reduce the chance of the hosts detecting that they have been parasitised" (p1520).

The researchers provided evidence for this view from three experiments in Cambridgeshire, England.

Experiment 1 (repeated measures design) - At 24 reed warbler (Acrocephalus scirpaceus) four different calls were played for 3-4 seconds each:

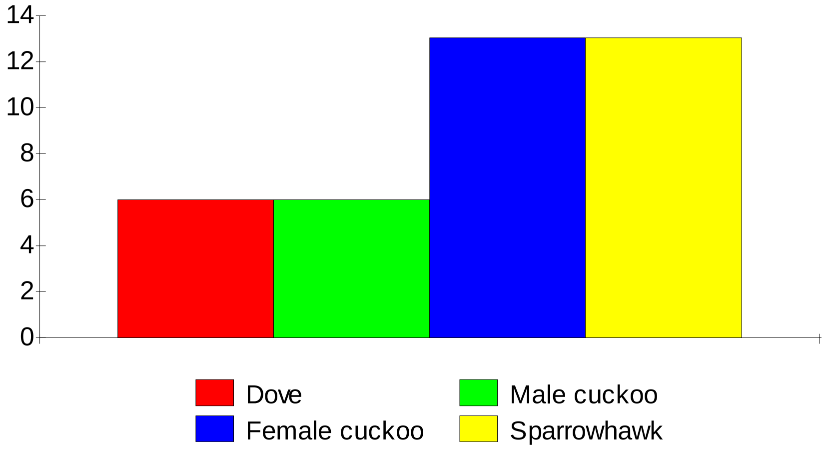
- F cuckoo (threat to clutch but not adult host);
- Male cuckoo (no threat, but parasitism cue);
- Collared dove (Streptopelia decaocto) (control);
- Eurasian sparrowhawk (Accipiter nisus) (threat to adult

but not clutch).

The response of the bird in the nest was observed (eg: vigilance - peering over nest rim for more than one second). The hosts responded with vigilance to both the female cuckoo and the hawk calls.

Experiment 2 (independent design) - The same four calls were played to sixty great tits (Parus major) and blue tits (Cyanistes caeruleus), who are not cuckoo hosts, at a peanut feeder. The tits responded in the same way to the female cuckoo and the hawk calls (ie: with vigilance). "As cuckoos are no threat to tits, their similar response to the calls of female cuckoos and hawks is likely to have resulted from perceived acoustic similarity" (York and Davies 2017 p1521).

Experiment 3 (independent design) - At 72 reed warbler nests, the researchers replaced a host egg with an obviously different ("non-mimetic") egg. A model cuckoo was placed near the nest and one of the four different calls was played. The nest was checked one and three days later to see if the false egg had been "accepted" (kept) or "rejected" (thrown out of nest). Reed warblers exposed to female cuckoo and hawk calls were more likely to accept the false egg after one and three days (figure 5.7).



(Data from York and Davies 2017 figure 2 p1523)

Figure 5.7 - Number of nests accepting false egg after one day based on call played [29].

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[29] Collared dove and sparrowhawk call played 18 times each, and others seventeen times.

5.8. CLEVER BEES

Associative learning (or classical conditioning) of reflexes has been studied in honeybees over many years (Abramson et al 2016). The proboscis extension reflex occurs in response to flower scents naturally, and can be conditioned to a particular unnatural smell (eg: Bitterman et al 1983). The sting extension reflex can be conditioned with an electric shock to occur in response to a certain smell also (eg: Vergoz et al 2007).

Operant conditioning is learning based on rewards and punishments to previous behaviour choices. It can be used to teach novel behaviours, as Abramson et al (2016) did with 55 honeybees in a laboratory.

The task to be taught was the pushing of a plastic lid off a well containing sucrose solution. The bees learned in one of three conditions - two shaping conditions and a control one. In the shaping conditions the bees were rewarded step-by-step for relevant behaviours (eg: touching the lid, then pushing it, then pushing it off the well). The bees were significantly quicker at learning in the shaping conditions than in the control condition (ie: three times faster). However, three-quarters of the bees in the control condition accessed the food by "happenstance". "These results suggest the strategies to access concealed food sources exist naturally, but experience can hasten the bee's mastery of such strategies" (Abramson et al 2016 p13).

5.8.1. Flexible Learning by Bees

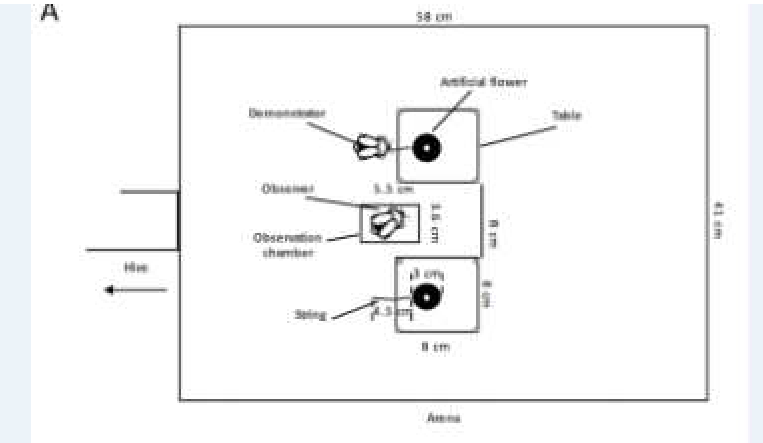
Thus, bees show the ability to perform a number of cognitive tasks, but many of the tasks used "have analogues in bees' natural foraging routines, and bees might perform well at them simply because the learning processes involved might be used in tasks encountered by bees naturally" (Loukola et al 2017 p833). Loukola et al (2017) used tasks not encountered in the wild to investigate the cognitive flexibility of bees.

In the first experiment, bumblebees were trained to push a small yellow ball on a circular blue platform through a hole for a sugary reward. Subsequently, in a test on a square platform, nine bees all succeeded in performing the task.

In the second experiment, bees were presented with three balls and the task was to push one ball in particular into the hole. Training took place in three conditions - (i) observing a previously taught bee doing the correct task (social demonstrator), (ii) the ball was moved by a magnet underneath the platform ("ghost" demonstrator), and (iii) no demonstration. Bees in the social demonstrator condition were most successful at learning to perform the task. This was evidence of social learning of a task that had no natural equivalent. More than that the bees did not just copy the demonstrator (pushing the ball), but used a more convenient strategy (eg: pulling the ball). "That bees solved this novel, complex goal-directed problem—and solved it via observation and using a better strategy than originally demonstrated — shows an unprecedented degree of behavioural flexibility in an insect" (Loukola et al 2017 p835).

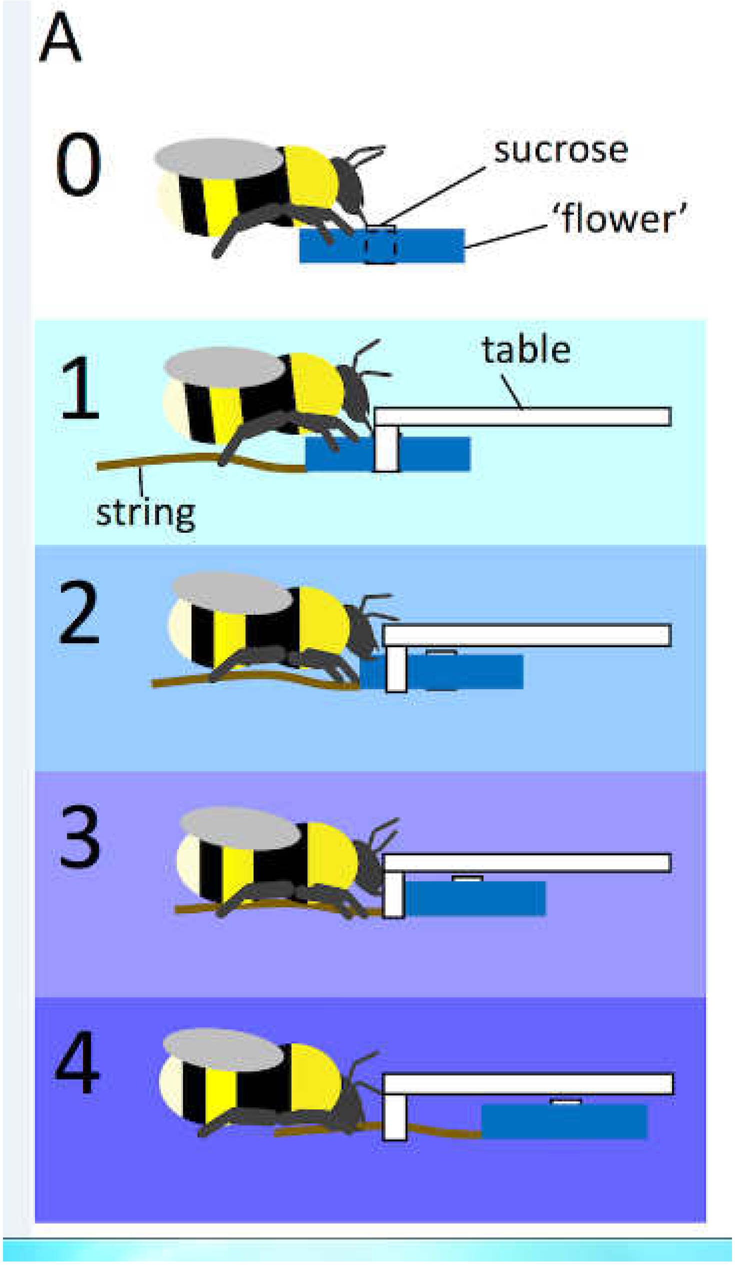
Alem et al (2016) also used a task not found in nature. Eleven colonies of bumble bees, that had learned that blue artificial flowers contained sucrose solution, were taught to pull a string to access the flowers. Individual bees watched either another bee ("demonstrator") pull the string (social observation condition), the researcher pull the string ("ghost control" condition), or no demonstrator (figs 5.8 and 5.9).

The bees were significantly better in a similar string pulling test in the social observation condition than the other two conditions (60% success vs 8% in control and 0% in "ghost control" conditions).



(Source: Alem et al 2016 figure 2A)

Figure 5.8 - Diagram of experimental set-up.



(0 = learning that blue flowers contain reward; 1 = 50% of flower covered by transparent table; 2 = 75% covered; 3 and 4 = 100% covered)

(Source: Alem et al 2016 figure 1A)

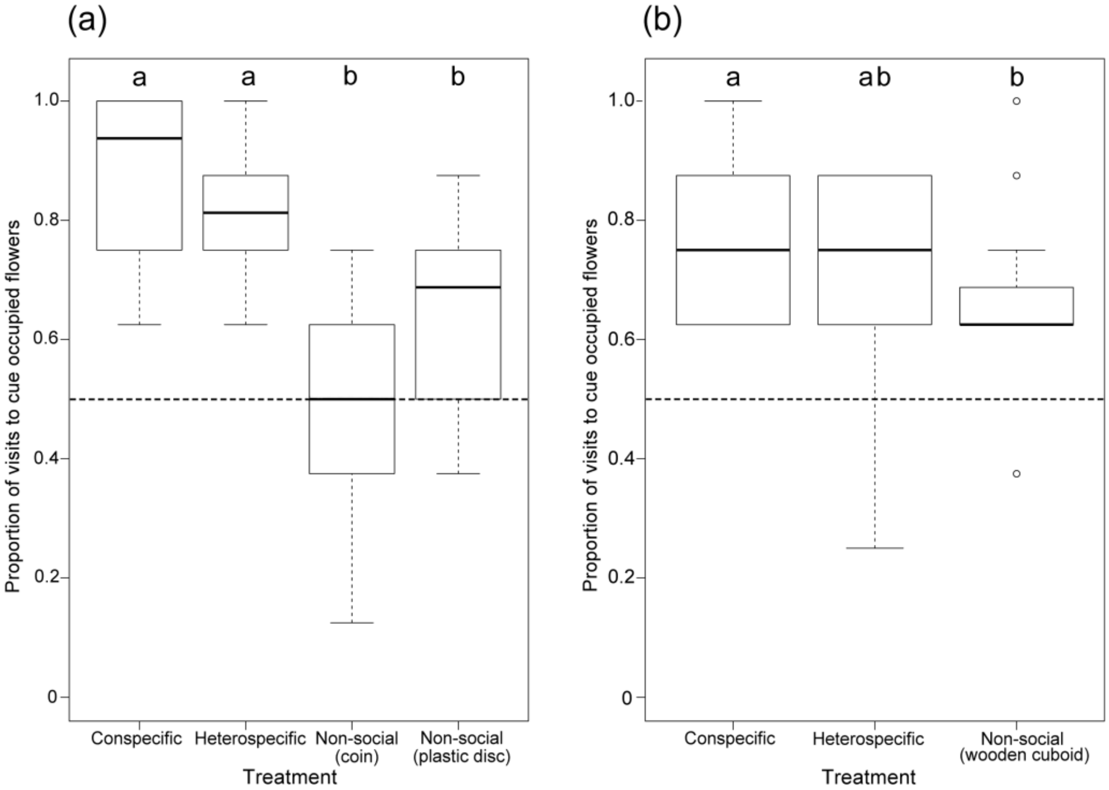
Figure 5.9 - Steps in behaviour shaping of bees to pull string.

5.8.2. Heterospecific Learning

Dawson and Chittka (2012) investigated experimentally whether bumblebees (Bombus terrestris) could learn from honeybees (Apis mellifera). Bumblebees learned that a single artificial yellow flower filled with sucrose solution was rewarding in different "demonstrator" conditions - either the presence of a bumblebee (dead) on the flower (conspecific social learning), a dead honeybee (heterospecific social learning), an object like a coin (non-social learning), or nothing (control).

The bumblebees were then tested with a choice of eight flowers, of which one included the demonstrator and the reward. The bees went to the correct flower significantly more often in the conspecific and heterospecific conditions (figure 5.10). This was also the case when the test used blue flowers after learning with yellow ones (transfer of learning test).

Dawson and Chittka (2012) concluded that they had "demonstrated that under similar learning conditions, heterospecific social learning is not only possible but also as efficient as that of conspecific social learning" (p5).



(Differences between a and b = significant; dashed line = chance)

(Source: Dawson and Chittka 2012 figure 1)

Figure 5.10 - Proportion of visits to correct flower in test for bumblebees with (a) prior experience of foraging or (b) not (including medians, interquartile range and maximum/minimum values).

5.9. NUMERICAL ABILITY

"Half a century ago, the assumption that the ability to perceive and reason about number was uniquely human was taken more or less for granted in all of the cognitive sciences... Experimental work in the last several decades has essentially reversed that assumption. There is now a broad consensus that the perception of numerosity and elementary numerical computation (the application of the ordering operation, ≥, for example) to number percepts are found even in arthropods" (Butterworth 2017 p2).

One numerical ability is the "size effect", which is the ability to distinguish two groups of objects based on the difference between then (eg: 6 vs 2 easier than 5 vs 6) (Butterworth et al 2017).

Basic counting has also been reported in real life situations. For example, male tungara frogs compete by coding more "chucks" in their calls than the previous caller. Males can "add up to 4-6 chucks to their advertisement calls, thereby showing evidence of counting to at least this number" (Rose 2017 quoted in Butterworth 2017).

5.10. ELEPHANTS FEAR BEES

African elephants respond negatively to the sound of African honeybees, as King et al (2007) showed in a playback experiment. The majority of eighteen elephants immediately (ie: within 10 seconds) walked or ran away at the sound of the buzz of disturbed bees (figure 5.11). A four-minute recording of bees or natural white noise (a waterfall recording) (control) was played from a speaker placed ten metres from the elephants at the Samburu and Buffalo Springs National Reserves in Kenya.

The sound of bees could be used to keep elephants from encroaching on human developments.

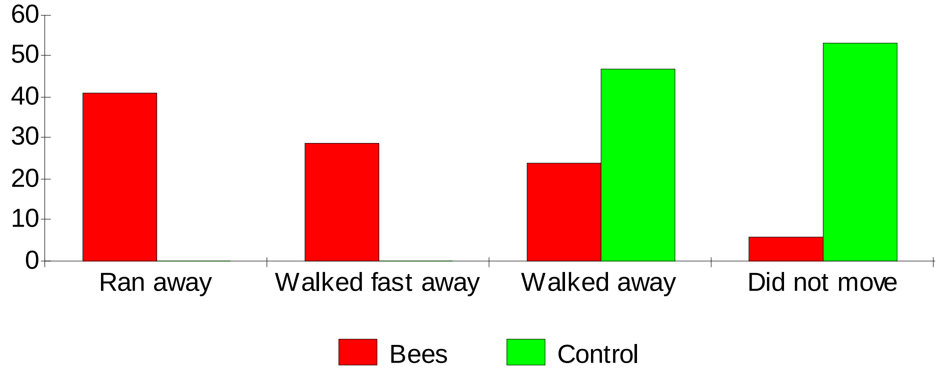


Figure 5.11 - Responses (%) of elephants to playback.

5.11. ROBBING AND BARTERING

"Across the globe, increasing human encroachment on natural habitats leads to a multiplication of contact zones where humans and other primate species live in sympatry and routinely interact" (Brotcorne et al 2017 p505). One example of this interaction occurs at Uluwatu Temple in Bali, Indonesia, where long-tailed macaques (Macaca fascicularis) are free ranging and live in close proximity to humans.

These macaques have been observed showing object robbing and object/food bartering (RB) behaviours. This sequence "usually occurs in two steps: after taking inedible objects (eg: glasses) from humans, the macaques appear to use them as tokens, returning them to humans in exchange for food" (Brotcorne et al 2017 p505) [30].

Brotcorne et al (2017) explained RB as "a feeding strategy which has emerged in ecologically flexible macaque species living in anthropogenic habitats... By relaxing foraging pressures, food provisioning gives the macaques some free time, and creates favourable environmental conditions under which behavioural innovations may emerge... Moreover, food provisioning attracts the macaques to open areas where tourists carry around a variety of objects. Such human-influenced environments increase opportunities to associate these objects with potential food rewards" (p506).

Brotcorne et al (2017) observed the RB behaviours at Uluwatu Temple formally between June and October 2010 with focal observation (20-minute samples watching one individual), and event sampling (recording details of all occurrences of RB). A total of 416 hours of observations. Four stable social groups of macaques (involving 66 individuals) were observed. Two groups ("Gading" and "Riting") spent a lot of time in tourist zones, and two groups ("Celagi" and "Melum") less so.

About a quarter of individuals were observed showing RB behaviours. In total, there were 201 events observed - 85% involved successful robbing, and of these, the vast majority ended in successful bartering. Glasses, followed by hats, were the most common objects taken.

The researchers tested three theories:

i) Environmental opportunity hypothesis - The

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[30] The exchange of an inedible object for food has been trained in experiments with macaques using reward tokens (eg: Addessi et al 2007). But Brotcorne et al (2017) are the "first to focus on the spontaneous expression of RB events (ie: the macaques initiate robbing events without any encouragement from humans), at least partially monkey-driven (ie: even though bartering events depend on the willingness of humans to exchange, the macaques can choose to barter or not), and exhibited by a large number of free-ranging individuals" (p506).

influence of the environment on behaviour, such that it was predicted that groups spending more time in tourist zones of the temple would show more RB behaviours. The data supported this prediction with a RB frequency of 0.60 events per hour for the Gading and Riting groups compared to 0.06 for the other two groups, for instance.

"In other words, the likelihood for the Uluwatu macaques to perform RB behaviours increased with opportunities to interact with humans. For young macaques growing up in this population, this could translate into more chances to learn about the affordance of the objects carried around by temple visitors, either by engaging in RB on their own (ie: individual trial-and-error learning), watching skilled group members rob and barter (ie: direct social learning via observation), or manipulating discarded tokens (ie: indirect social learning via stimulus enhancement). Repeated exposure to favourable environmental conditions (ie: temple visitors carrying around inedible but valuable objects) provides opportunities for the Uluwatu macaques to practice RB with humans" (Brotcorne et al 2017 p513).

ii) Male-biased sex ratio hypothesis - RB behaviours are risky, and so adult males are predicted to engage in them more than females. Groups with more males will show more RB behaviours overall. There was partial support for this prediction. For example, two groups with similar sex ratios showed significant differences in RB frequency.

iii) Group density hypothesis - Novel behaviours spread more widely in groups of higher density. This prediction was not supported by the data as the group with the highest density had a lower RB prevalence.

Brotcorne et al (2017) drew the following two conclusions:

- RB is a spontaneous, customary and enduring practice among groups at the Uluwatu Temple interacting with humans.

- RB is not observed in other Balinese macaques where there is opportunity (eg: Pulaki Temple) (persona observation by Leca and Gunst 2010 in Brotcorne et al 2017).

Brotcorne et al (2017) ended: "Even though there is a need for a more systematic assessment of the local ecological and anthropogenic conditions in these populations, our findings indicate that RB is a good candidate for a new behavioural tradition defined as a group-/population-specific practice, socially transmitted among at least some group members, persistent over several generations, and possibly locally adaptive" (p514).

5.12. APPENDIX 5A - DRUMMING AS COMMUNICATION

Vibrational communication covers the drumming of a part of the body on the ground, tree or other substrate. Among mammals, the body parts include the foot (most commonly), the head or the teeth, and among rodents most commonly (Randall 2001). Vibrational communication is unique because it can be transmitted through two channels - the air and the ground [31].

Concentrating on foot-drumming, Randall (2001) outlined five main communication contexts:

- Territorial occupation
- In aggressive interactions
- Mating interactions
- To communicate subordinance
- Danger from predators.

In terms of its evolution, foot-drumming may be an extension of foot digging behaviour, or a displacement behaviour when faced with a threat. "An animal may experience conflicting urges when encountering a threat: either move toward the object of the threat and inspect it to gain more information or run away and escape and hide" (Randall 2001 p1144).

Foot-drumming is seen most strongly in the banner-tailed kangaroo rat (Dipodomys spectabilis), where both sexes perform it, and individuals have distinct signatures (Randall 2001). Using playback recordings, Randall (1994) found that individuals of this species could distinguish territorial neighbours from non-neighbours, with unfamiliar foot-drumming producing a faster response of foot-drumming.

5.13. APPENDIX 5B - SOMA AND MORI (2015)

Male Java sparrows (Lonchura oryzivora) produce bill-click sounds along with songs during courtship displays (directed singing) and when singing alone (unidirectional singing). Females have also been observed to produce bill clicks (Soma and Mori 2015).

Soma and Mori (2015) analysed the recordings of

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[31] In terms of the problem of amplification, Jonsson et al (2017) reported that male crickets (Acanthacara acuta) increased the loudness of their calling by forming a chamber covering the wings with an inflated pronotum (the plate covering the thorax area). The call is produced by stridulating with the forewings.

unidirectional singing by thirty domesticated males in Japan. All the males produced songs with bill clicks, even individuals raised in isolation, but not all songs included bill clicks (around 60% did). "Older birds produced bill clicks during almost every song bout, while younger adults did not, suggesting that bill clicks continue to be added after song crystallisation at around the age of 6 months. Moreover, fathers and sons showed a similar rate of clicks..., which suggests that the observed individual variation is not random, but rather depends on social learning or genetic inheritance" (Soma and Mori 2015 p6) [32].

Subsequent analysis suggested that bill clicking is inborn, but the pattern of bill clicking and the integration with song notes is learned.

Integrating visual and auditory signals (multi-modal communication) in courtship displays has been observed in other birds (eg: synchronised expanding of wings and song in male brown-headed cowbirds; Cooper and Goller 2004; or the co-ordination of dance and song by male superb lyrebirds; Dalziell et al 2013).

5.14. APPENDIX 5C - TOOL USE IN OTHER SPECIES

Tool use is important in helping a species to adapt to climate change and the effects of humans on the natural environment. Tool use is an example of behavioural plasticity, "which permits individuals to adjust rapidly to local changes ahead of any phenotypic adjustments" (Luncz et al 2017 p873).

Luncz et al (2017) reported their observations on a group of wild long-tailed macaques (Macaca fascicularis) in Thailand, who had adapted their behaviour of cracking shellfish to oil palm nut cracking. The food item was placed on a flat surface ("anvil") and hit with a small rock ("stone hammer"). The researchers recorded the macaques with camera traps over three weeks in 2016.

Luncz et al (2017) summed up: "Compared to their known exploitation of marine prey, this is a relatively short time span for the macaques to learn to exploit this novel food source. We hypothesise that long-tailed macaques have transferred an existing technological solution of harvesting encased shellfish within a coastal environment to exploit the nutritious nut of palm oil trees within an inland setting" (p878).

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[32] Social learning is key to cultural transmission, and it is assumed that this depends on exact copying, but Truskanov and Prat (2018) argued that it is a "widespread misconception that high fidelity of transmission depends on precise copying of cultural information and suggest the opposite: fidelity of transmission might depend on inexact copying, coupled with trial-and-error exploration, which together allow flexibility in applying a learned behaviour and tailoring it to the current environment" (Kolodny et al 2018 p1).

5.15. APPENDIX 5D - INTERVAL TIMING IN DIFFERENT SPECIES

Bumble bee (Bombus impatiens) (Bolsvert and Sherry 2008)

Sixteen females were trained to extend their proboscis through a hole to receive a sucrose reward when a light went out in an experimental chamber. The bees were classically conditioned to associate the light going out with an immediate reward. Interval timing (ie: "sensitivity to the duration of time intervals") was tested by delaying the reward for a certain time (6, 12 or 36 seconds) after the light was turned off. The bees were tested on one interval per session (independent timing) or two different intervals per session (multiple timing). Both groups waited for the reward for the shorter time intervals (eg: six seconds), but the independent timing group were significantly more likely to wait for the longer time interval (36 seconds). The results showed that bumble bees can learn to time interval durations.

Cats (Rosenkilde and Divac 1976)

Fourteen cats were presented with two feeders which could be accessed when a cage door was opened. They were initially trained to eat from both feeders and to return promptly to the cage. The time period in the cage was 1-2 seconds. Discrimination of time was tested by varying the length of confinement in the cage (5 or 20 seconds) (independent variable), and which feeder to approach (right after five seconds and left after twenty seconds). Approaching the correct feeder was scored as a hit (dependent variable). The time intervals were subsequently varied (eg: 5 vs 18 seconds; 5 vs 8 seconds).

All the cats could discriminate between five and twenty seconds, but only seven cats could 5 from 8 seconds.

Goldfish (Drew et al 2005)

Thirty-six goldfish learned to associate a light coming on with a mild electric shock with a five-second or fifteen-second gap between the two. After training, the fish showed a response to the light 5 seconds after (five-second condition) or 13 seconds after (fifteen-second condition). This suggested the perception of short time intervals.

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6. SLEEP AND NON-HUMAN ANIMALS

6.1. ELEPHANTS

Sleep in animals is often studied in captive individuals. So, for example, captive elephants sleep for three to seven hours per day (In Brief 2017). The first study was of circus elephants (Benedict and Lee 1938), and thee researchers made the observation that the "degree of trunk movement may well be taken as an index of whether the animal is asleep or awake" (quoted in Gravett et al 2017) [33]. But captive animals may not be representative of wild individuals.

Gravett et al (2017) found twelve previous studies in their literature review, of which nine were captive animals (table 6.1).

Type of study	Number of studies	Hours of sleep
Captive - zoo	6	2-4 hrs; 4 studies not reported
Captive - circus	2	6 hrs; 1 study not reported
Captive - both	1	3-7 hrs
Wild	3	3-4 hrs; 2 studies not reported

(Based on Gravett et al 2017 table 1)

Table 6.1 - Types of study of sleep in elephants.

Overcoming the practical problems, Gravett et al (2017) studied sleep in elephants in Chobe National Park, Botswana, by fitting motion sensors to the trunk. Lack of movement for a five-minute period was categorised as sleep. Two older females monitored for thirty-five consecutive days slept for an average of two hours per day (mostly between 2 am and 6 am) in four or five short bursts (ie; the sleep was polyphasic). The risk of predation and the need to eat for so many hours per day seem to be key here.

On five occasions the elephants went 48 hours

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[33] Elephants have been observed to rest/sleep while standing, with the end of the trunk on the ground and their eyes closed (Gravett et al 2017).

without sleep when travelling.

There was evidence that the elephants occasionally laid down to sleep, which would be the only opportunity for REM sleep, it was speculated. REM sleep has been found in most mammals studied, however elephants are closely related to manatees and hyraxes (Afrotherian mammals), which show great variance in sleep architecture and states. For example, the Amazonian manatee, which is fully aquatic, spends 1% of the average seven hours of total sleep in REM, while the rock hyrax spends even less time in REM sleep and has a novel sleep state (Gravett et al 2017).

Elephants have two novel brain structures in the hypothalamus and pons (compared to other mammals), and Gravett et al (2017) speculated that "if polysomnographic recordings of sleep in the elephant were undertaken, novel sleep states, associated with slow wave or REM (REM may form a very small portion of TST [total sleep time] in the elephant), may be present in the elephant" (p26).

6.2. PINNIPEDS

Sleep in pinnipeds has been studied in captive animals mostly. Fur seals, for instance, have been observed to sleep at the surface on their sides holding their nostrils above the water and paddling continuously to maintain this position. This is unihemispheric sleep (Karamanlidis et al 2017).

"True seals" that can hold their breath (eg: grey seals) can sleep while floating motionless at the surface or at depth (in a horizontal position or a vertical "bottling" position), or lying at the bottom of a pool. Sleep occurs here in both brain hemispheres simultaneously (Karamanlidis et al 2017).

Karamanlidis et al (2017) reported six observations of the Mediterranean monk seal (Monachus monachus) showing this behaviour in the wild. Four observations were of adults lying on their belly on the sea bottom.

6.3. UNIHEMISPHERIC SLEEP

There is a trade-off with sleep between its benefits versus reduced vigilance. One evolutionary solution is unihemispheric sleep, as seen in birds and aquatic mammals (eg: cetaceans, walruses). "During unihemispheric sleep, brain activity measured by an electroencephalogram shows a pattern characteristic of sleep in one hemisphere, while the other hemisphere shows brain waves more closely resembling wake-related activity. This between-hemisphere difference in brain state is reflected at the level of the eye by unilateral eye closure (UEC), with the eye neurologically connected to the 'awake' hemisphere being open" (Kelly et al 2015 p3175).

The direction of gaze of the open eye varies. Ducks, for example, on the edge of a group orient their open eye to look for predators (while individuals in the middle of the group sleep bihemispherically), as do lizards who orient towards the last known location of a threat. But crustaceans keep their open eye on pod members to maintain cohesion (Kelly et al 2015).

Kelly et al (2015) studied experimentally unihemispheric sleep in three juvenile saltwater crocodiles (Crocodylus porosus) using UEC over 24 hours in Australia. In a tank surrounded by eight video cameras, an individual crocodile was placed in a 12-hour light/dark regime. Another crocodile was in sight in another tank to test if the open eye would orient towards that direction (like cetaceans). Also a human appeared for ten minutes to stand by the tank to test if the open eye would orient towards them (like ducks).

Video recordings were scored per second as bilateral eye opening, UEC, bilateral eye closure, or unclear. UEC was further scored as which eye was open, and the orientation of that eye. Baseline measures were made before the other crocodile was introduced or the human appeared.

At baseline, bilateral eye closure was most common, especially at "night", followed by bilateral eye opening, then UEC. The researchers reported that this was the first report of UEC in saltwater crocodiles, along with previous reports in the caiman and Nile crocodile.

The introduction of another crocodile in sight did not increase the amount of UEC compared to bilateral eye closure, but the open eye was directed significantly more towards that crocodile. "Such a function could well have ecological relevance in crocodiles, as hatchling saltwater crocodiles form creches in the wild as an anti-predator adaptation. Animals best able to maintain group cohesion may have a greater chance at survival" (Kelly et al 2015 p3176).

UEC increased with the presence of the human, and "the open eye was always directed towards the human, an effect that persisted even after the human had left the room" (Kelly et al 2015 p3176).

The researchers explained their findings in relation to unihemispheric sleep: UEC "might suggest that crocodilians engage in unihemispheric sleep. If true, then unihemispheric sleep is likely to have been present in the most recent common ancestor to archosaurs (crocodilians and dinosaurs, including birds), and given the phylogenetic breadth of UEC across reptiles..., may have evolved even earlier, perhaps in the ancestor to Sauropsids (avian and non-avian reptiles) or in the stem amniote with a subsequent loss of the state in the ancestor to mammals. Alternatively, and equally interesting, is the possibility that UEC first evolved in early Sauropsids for a purpose beyond that of sleeping unihemispherically, perhaps related to focusing visual acuity and attention in a lateralized brain... and/or eliminating superfluous parts of a visual field in animals with laterally placed eyes... Birds then evolved the ability to enter sleep with the hemisphere associated with the closed eye as a derived feature of sleep. If true, then unihemispheric sleep may have first evolved in the archosaur lineage with the appearance of birds by elaborating upon a pre-existing behaviour inherited from a common ancestor with non-avian reptiles" (Kelly et al 2015 p3177).

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7. COMMUNICATION

7.1. INTRODUCTION

Bradbury and Vehrencamp (1998) outlined the key features of any communication system, including:

a) Signal range - Distance between sender and receiver.

b) Locatability - eg: mating signals need to show where the sender is.

c) Duty cycle - The period of "on" and "off" of the signal.

d) Identification level - Who understands the signal (eg: kin only).

e) Modulation potential - The ability of the signal to be adapted for individual variation.

f) Form-content linkage - The link between the sender and the signal (ie: honesty of the signal) (eg: large animals make louder calls).

Communication is most commonly used to find a mate as seen in species where females who search often lack songs compared to signalling males (eg: crickets, katydids, anurans, songbirds) (Bradbury and Vehrencamp 1998).

7.2. CHEMICAL SIGNALS

Chemical signalling by mammals occurs with urine and faeces, and specialised scent glands around the body (eg: face, feet, anus). Such signals have longevity (ie: last over time) in a way that auditory and visual signals do not.

This is important for species that are mostly solitary, and move around a lot (non-territorial), like bears. For example, tree rubbing by brown and black bears leaves scent that communicates dominance status (Sergiel et al 2017).

Sergiel et al (2017) focused on the pedal glands (paws) of wild brown bears (Ursus arctos) captured in the northern Carpathians (southern Poland), and from observations in the Cantabrian Mountains (north-west Spain) between 2012 and 2015 (using video-recording camera traps).

Pedal marking behaviour was observed as "a characteristic gait while walking [34], carefully stepping and twisting their feet in depressions made in the ground... by the repeated use of the marking site along time" (Sergiel et al 2017 p4), and by the sniffing of pedal marks by others.

In terms of the chemistry of the scent, Segiel et al (2017) found differences between adult males and females, which would suggest pedal marking for sex recognition. For example, Owen et al (2014) reported that polar bears spent more time sniffing pedal scent from the opposite sex.

7.3. CROSS-SPECIES PLAYBACK

Lingle and Riede (2014) observed that the "distress vocalisations or cries of newborns are remarkably similar across mammals, including humans" (p510). These include separate calls (also known as attraction or isolation calls), and distress or capture calls (given under predator attack) (Lingle and Riede 2014). Newman (eg: 2007) proposed "an integrated system that has been conserved throughout mammalian evolution and encompasses not only the production of cries but also the perception and processing of cries leading caregivers to respond (Lingle and Riede 2014 p510).

This can be seen in humans responding to distress calls of domestic animals, like dogs, and vice versa (Lingle and Riede 2014).

The common characteristics of calls include the fundamental frequency, the call duration, and call rate, and to "test whether vocalisations contain shared elements that are capable of eliciting a response across species, one first needs to control for species-specific traits" (Lingle and Riede 2014 p511). Aubin (1991), for example, has done this with different species of birds.

Concentrating on mammals, Teichroeb et al (2013) played infant distress calls of mule deer (Odocoileus hemionus) and white-tailed deer (Odocoileus virginianus) to the opposite mothers, who responded only if the fundamental frequency "remains within a certain species-specific range, hereafter the 'frequency response range'"

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[34] This gait has been called "stomp walking" or "sumo strutting" (Clapham et al 2014).

(Lingle and Riede 2014 p511) (ie: 400-1400 Hz for mule deer and 300-800 Hz for while-tailed deer).

Lingle and Riede (2014) built on this research, and played a variety of distress calls (including sea lions, bat, human, and domestic dog) to mule and white-tailed deer mothers in wild populations in Alberta, Canada. The response of the mother to the sound was scored by observers as alert, approach or retreat in relation to the playback speaker.

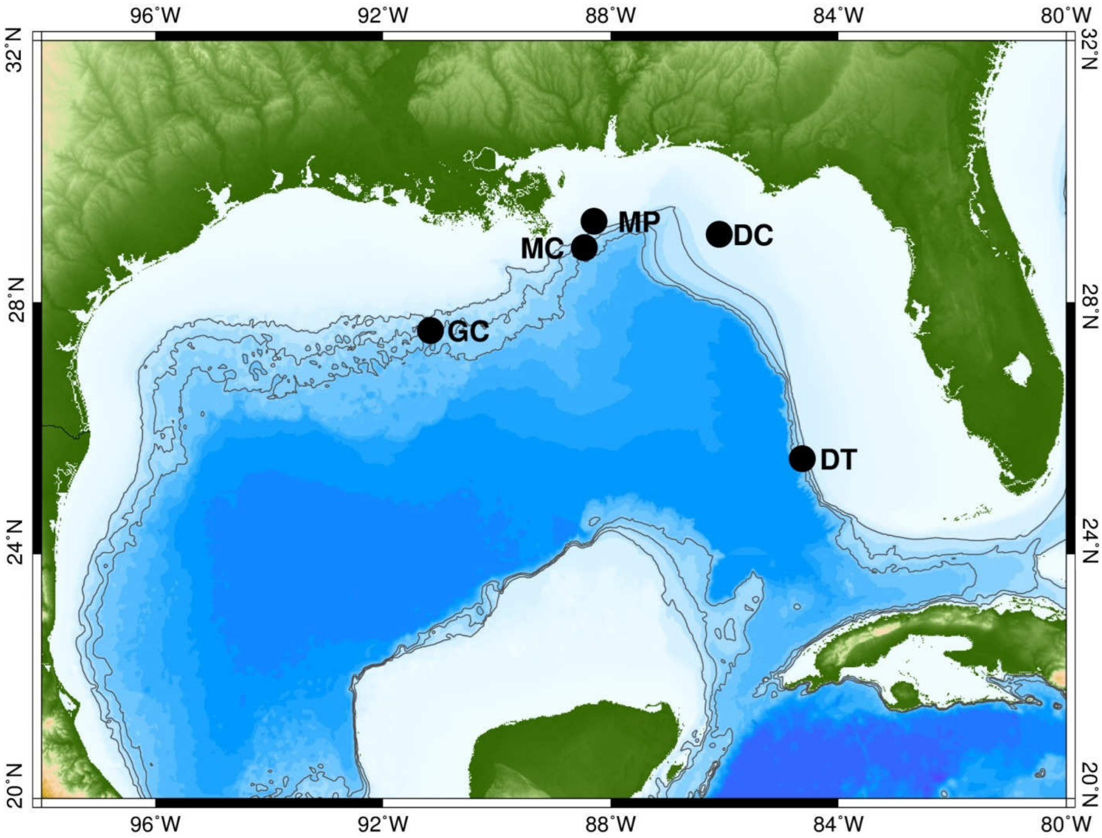
The mothers responded to the newborn calls (ie: moved towards the speaker) if they naturally fell within the deer's fundamental frequency or had been manipulated to do so.

Lingle and Riede (2014) commented: "From an adaptive perspective, a hard-wired response to newborn distress vocalisations can be considered a classic example of a speed-accuracy trade-off..., in which it pays to respond, in case the newborn in distress is one's own offspring, rather than delay action until confirming the animal's identity, for such a delay could increase the risk of the infant being harmed or killed" (p519).

7.4. ECHOLOCATION CLICKS

Dolphins use echolocation clicks while socialising, foraging, and travelling. Classifying these clicks can be done by trained humans, while Frasier et al (2017) used an automated system. High-frequency acoustic recording packages (HARPs) were left in five seabed locations in the Gulf of Mexico between 2010 and 2012 (figure 7.1). The data collected by the hydrophones (52 million clicks) were analysed by algorithms designed to spot patterns. The aim was to recognise dolphin species by clicks.

Seven distinct click types were identified, of which one was known to be associated with Risso's dolphin (Grampus griseus) (based on recordings from other studies, and observations by the researchers of this study). The others were not identified as clearly.



(Green/brown represents land, and white/blue represents water. The five sites are named based on the US federal lease block in which they are located: Mississippi Canyon (MC), Green Canyon (GC), Dry Tortugas (DT), DeSoto Canyon (DC) and Main Pass (MP))

(Source: Frasier et al 2017 figure 6)

Figure 7.1 - Location of HARPs in Gulf of Mexico.

7.5. LANGUAGE AND APES

Great apes are traditionally viewed as incapable of vocal learning (ie: "the capacity to expand their vocal repertoire with new calls learned from others"; Lameira et al 2016), as seen in "great ape language projects". These were attempts to teach trained captive individuals new word-like utterances have failed (Lameira et al 2016). For example, "Gua" (chimpanzee) raised as their own child by Kellogg and Kellogg (1933) made no utterances, while "Viki" (chimpanzee) could say four words after three years (Hayes 1951).

For Lameira et al (2016), the problem with these projects was that "great apes' vocal skills were directly compared with humans', rather than objectively against their own natural vocal preferences, predispositions, and limitations" (p1). These researchers showed that an adolescent captive male orang-utan called "Rocky" could produce new "wookie" vocalisations (ie: expand their vocal repertoire). Based at Indianapolis zoo, this individual copied new "wookie" sounds modelled by a human demonstrator. "These results confirm the capacity of orang-utans to learn and acquire new calls into their individual repertoires, both in the form of voiceless consonant-like calls and voiced vowel-like calls" (Lameira et al 2016 p7). These require vocal fold control (or volitional voice control; Pisanki et al 2016).

The implication of this finding is that spoken language emerged earlier in the evolutionary timeline than the genus Homo. "Full articulatory range and excellent vocal control as observed today in humans may be relatively recent within the human lineage. However, the presence of learned consonant- and vowel-like calls, potentially as far as 10 mya [million year ago] within our lineage, allows considering gradual forces and progression in stages towards full-blown language" (Lameira et al 2016 p8).

7.6. VESTIGIAL BEHAVIOUR

Schneider et al (2018) described an example of "evolution at work" in the Hawaiian field cricket (Teleogryllus oceanicus). Certain males [35] carry a genetic mutation in the wing development (flatwing), which means that they cannot make the usual call by "rhythmically opening and closing their forewings, scratching the scraper of one wing against the file of the other" (p1). This has an advantage in relation to an acoustically orienting parasitoid fly "whose larvae burrow into, consume and kill their host" (p1).

The males still make the original movements (vestigial signalling) despite producing no sounds. "Silent singing" is energetically costly, and such behaviour may be "co-opted for novel functions" in evolutionary time. For example, "vibration-duetting courtship behaviour of Lebinthine crickets may have arisen from a behaviour originally used for predator avoidance..." (Schneider et al 2018 p3).

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[35] 95% of males on Kauai island and 50% on Oahu (Schneider et al 2018).

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8. MISCELLANEOUS

8.1. PLAY IN NON-MAMMALS

Play can be defined as "a behaviour that is voluntary, repeated several times, doesn't have an obvious function (so running for fun, yes, but not running away from a predator) and differs in significant ways from regular, functional behaviour. It is also initiated by healthy, largely unstressed animals" (Zaraska 2017 p56).

Graham and Burghardt (2010) clarified five criteria to identify behaviour as play:

i) Not functional in the context in which the behaviour appears - eg: frogs wrestling irrespective of sex vs males wrestling for females (Burghardt 2015).

ii) Spontaneous, voluntary, and pleasurable.

iii) Different to the serious version of the behaviour - eg: pond turtles engage in foreclaw titillation displays in social interactions as hatchlings, which is behaviour shown by adults in sexual and aggressive encounters (Burghardt 2015).

iv) Repeated, but not in unvaried stereotypic way.

v) Appears when the individual is not stressed - The Surplus Resource Theory explains that "the origins of play are found in animals with sufficient metabolic resources for sustained activity and complex behaviour that needs to be deployed in varying ways. They also need the time and safety to engage in behaviour that may not be immediately advantageous, but through which animals learn or perfect behavioural skills, social acumen, physiological or perceptual abilities, and other means that enhance survival compared to non-playing conspecifics" (Burghardt 2015 pR10).

It has been assumed that only mammals participate in play, but studies are increasingly showing that this is not the case. Here are two examples.

Burghardt et al (2014) reported play behaviour by three captive cichlid fish (Tropheus duboisi) filmed over a two-year period. The fishes housed individually all showed a behaviour of hitting with the head a bottom-weighted thermometer. Each individual had their own style of thermometer-attacking behaviour.

Applying Graham and Burghardt's (2010) criteria for play to this behaviour:

- No functional benefit to the behaviour.
- Spontaneous and voluntary behaviour.
- Different behaviour to that might occur in fighting.
- Behaviour repeated.
- All fish in non-stressful situation.

Burghardt et al (2014) tried to explain this behaviour. The behaviour is not related to feeding as the fish is an algae gleaner, and it was not triggered by novel objects outside the tank. It was not related to courtship, but sometimes occur after the presence of a fish in another tank (ie: redirected aggression; appendix 8A).

The researchers favoured stimulus deprivation or boredom of a socially isolated fish as thermometer-attacking did not occur in a social tank.

But why were other objects in the tank not attacked? Burghardt et al (2014) asked, "was there something unique about the thermometer?". They answered, "probably, the most salient feature of the thermometer was its 'reaction' or response - it bounced back after being knocked..." (Burghardt et al 2014 p6).

A final puzzle was that "all other fish presented with this kind of thermometer that JBM [one of researchers] has used in keeping dozens of species, singly and in groups, over decades, have never reacted in ways as consistent and fascinating as did T. duboisi" (Burghardt et al 2014 p7).

Osvath and Sima (2014) studied play in juvenile common ravens (Corvus corax) in the context of emotional contagion - ie: "if a category of play in one individual induces a different category in another, this suggests the spread of a playful mood rather than released, species-specific behaviour" (Osvath and Sima 2014 p198)

[36]. Ravens have complex play behaviours, including social, object, and locomotor play.

Seven captive ravens at a Swedish university were observed over 48 days in three conditions:

- Baseline - measured play behaviours without objects or food.
- Food - play behaviours when food present.
- Toy - eg: large plastic insects, small stuffed toy.

In the analysis of the video-recordings, "object play" was defined as manipulation of the object, "locomotor play" included "lying on the side or back, hanging in beak or feet from elevated structure, and play flight", "social play" included "co-manipulation of small object, holding one leg of the other with one's foot, and lying on the side or back next to one another (co-lying)".

Play generally and individually two types of play (social and locomotor) were recorded significantly more often in the toy condition than the other two conditions. There was evidence in the toy condition of one type of play leading to another type. But the researchers admitted that the "precise details of the contagion process remain unclear" (Osvath and Sima 2014 p203).

8.2. CAVE-DWELLING CROCODILES

Crocodiles are found mostly in rivers. However, a few crocodilian species use caves for daytime or dry season refuge (eg: Chinese alligator), or nest guarding (eg: mugger), while three species are known to use caves more commonly (eg: Ankarana Caves Nile crocodile) (Shirley et al 2016).

Shirley et al (2016) added the African dwarf crocodile (Osteolaemus tetraspis) (figure 8.1) in west Central Africa. The researchers made observations in the Abanda cave system in Gabon in August 2010 and 2011 (at end of the dry season). Thirty-one crocodiles were captured and examined.

These crocodiles appeared to be "foraging exclusively in the caves" based on their stomach contents - bats and cave crickets. Shirley et al (2016) noted that "these primary cave prey sources are available year round with seemingly little seasonal variation in abundance or availability. This would be in stark contrast to prey availability in the forest habitats, which decreases

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[36] "Contagious play" has been observed in the rapid facial mimicry in orang-utans, for example, while social play increases when a playful individual rat is placed with a less playful individual (Osvath and Sima 2014).

(Source: Arpingstone; in public domain)

Figure 8.1 Captive African dwarf crocodile.

in availability in the dry season when the forest stream network is dry, for example" (Shirley et al 2016 pp418-419).

As well as this advantage, dwarf crocodiles in the surrounding forest stream network are hunted for bushmeat, and trees are being cut down by logging companies.

8.3. MOTOR LATERALITY AND CATS

Motor laterality is the preference for use of one limb over another as seen most obviously in human handedness (eg: 90% prefer to use right hand) (McDowell et al 2018).

What about non-human animals? Lateralised motor behaviours have been reported in primates, rodents, and amphibians, for example, in experiments involving forced choice tasks like food reaching, as well as in observations of spontaneous behaviours in the wild (eg: chimpanzees and grooming) (McDowell et al 2018). However, Warren (1980) argued that laterality is an artificial phenomenon created in forced task experiments, and so is less important in spontaneous behaviours.

McDowell et al (2018) investigated the differences in paw preferences of forty-four pet cats in experiments and spontaneous situations. The experiment involved retrieving food through a hole with one paw on fifteen trials, while naturalistic observations were made of three spontaneous behaviours - lying side, leading paw when stepping down a flight of stairs, and stepping over an object.

In the experiment, significantly more cats than chance (73%) had a paw preference, and likewise for two spontaneous behaviours (stepping down 70% of cats; stepping over 66%), but not lying side. There was no preference for left or right paw. The findings challenged Warren's (1980) argument, and suggested that "limb use on a forced experimental challenge may not be an artificial phenomenon, but may, rather, be an ecologically reliable indicator of motor bias for the domestic cat" (McDowell et al 2018 p41).

8.4. ENDANGERED SPECIES

Endangered species with small populations face the challenge of limited genetic diversity. Ang et al (2016) showed this was the case with the Tonkin snub-nosed monkey (TSNM) (Rhinopithecus avunculus) (figure 8.2), which is placed in the top 25 most endangered primates. The global population is estimated at less than 250 individuals (Ang et al 2016).

The study population was around 130 individuals in Khau Ca forest, Vietnam [37], and DNA was analysed from 254 faecal samples. There was around 98% similarity between individuals in the DNA analysed. "While some species with low genetic variation appear to be able to persist (eg: black-footed ferrets...), loss of genetic variation is often associated with increased extinction risk (eg: Tasmanian devil...)" (Ang et al 2016 p452).

Widespread deforestation and intensive hunting has meant that 90% of Vietnamese primate groups are endangered or critically endangered. Snub-nosed species generally are endangered (eg: around 2000 individuals of black snub-nosed monkeys; 800 individuals of grey snub-nosed monkeys) (Ang et al 2016).

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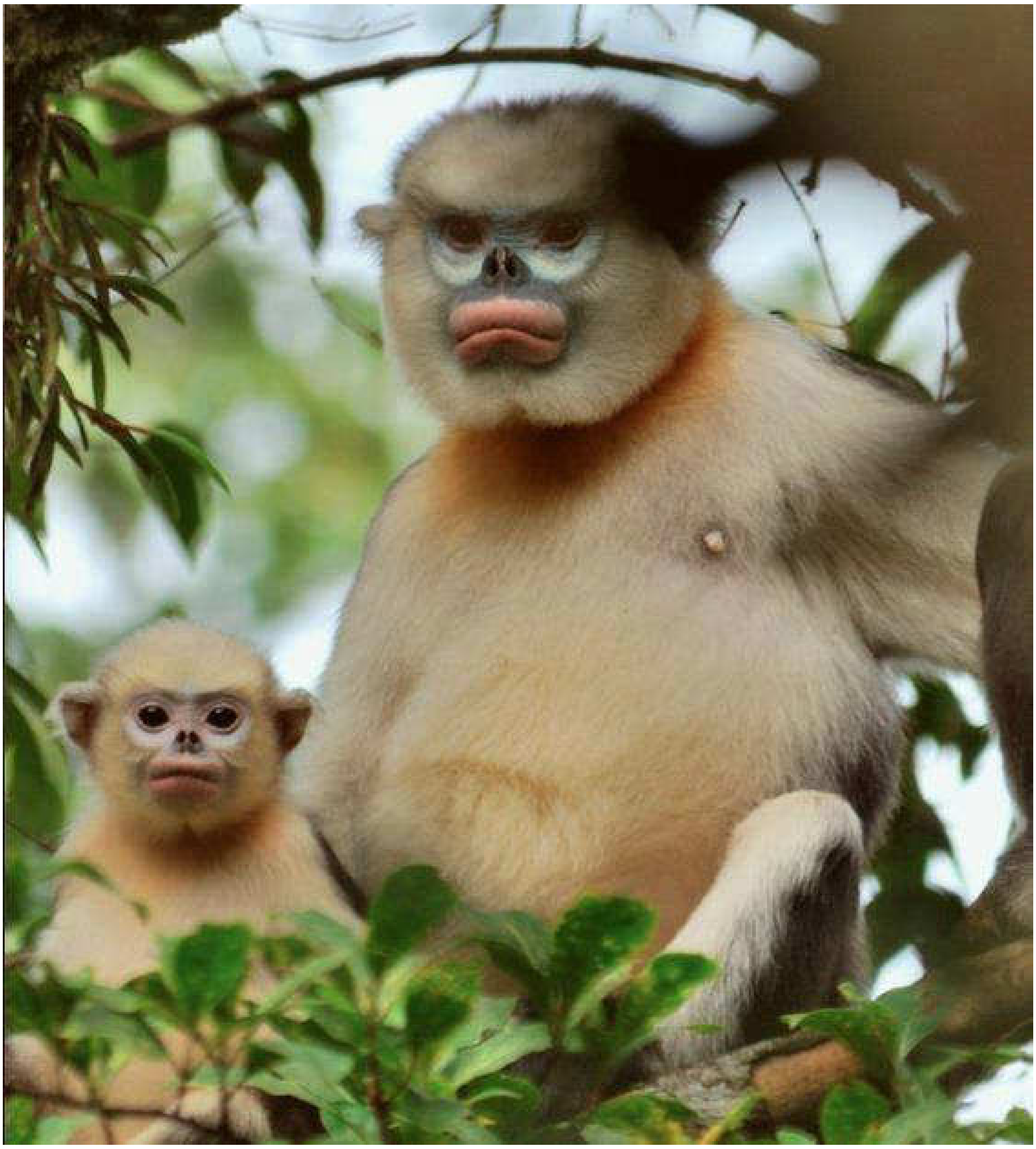
[37] This population was discovered in 2002, and another population in Vietnam in 1989 after fears of extinction about the TSNM (Ang et al 2016).



(Source: Paulo Henrique Foxer; in pubic domain)

Figure 8.2 - Tonkin snub-nosed monkey.

8.5. AUTOTOMY AND REGENERATION

Autotomy is a self-preservation technique where lizards and salamanders, for example, will lose a limb to a predator to survive. This goes hand in hand with the ability to regrow limbs (regeneration) (Gupta 2016).

The ability to regenerate may be linked to the immune system. As animals evolved, the ability to regenerate is lost as a more complex immune system developed a scarring response to injury to protect against infection. This is a "quick fix" compared to the slow regeneration process (Gupta 2016).

The regeneration process appears to be linked to dedifferentiation. After amputation of a limb, say, adult cells elsewhere in the body revert back to embryonic cells than can migrate to the inured area and start growing the new limb (Gupta 2016).

8.6. CITIZEN SCIENCE AND DOGS

Finding a large sample is always an issue for researchers, and Stewart et al (2015) described a citizen science project to test the cognitive abilities of pet dogs based on a website called "Dognition" [38].

Volunteers were instructed how to perform ten cognitive tests on their dogs. For example, placing a treat (unseen by the dog) under one of two cups and pointing to the correct one (arm pointing experiment).

Data from 500 individuals were analysed. The amount of correct responses were similar to previous researcher-led studies - eg: arm pointing 66% correct (vs Gasci et al 2009: 68% of 180 dogs).

Stewart et al (2015) admitted: "By definition citizen science is going to produce a qualitatively different type of data than conventional laboratory approaches. In addition, each discipline will face its own unique challenges implementing citizen science research. Our citizen science program was designed to take in to consideration the challenges that participants might have in conducting behavioural experiments reliably. We only included cognitive exercises that naïve volunteers showed skill at completing during pilot observations based on our instructions and written FAQs [frequently asked questions]".

They continued: "Like many other citizen science projects, our data seems to be of sufficient quality that it will help suggest where hypothesis driven research in more conventional research laboratories can be directed to either confirm or extend findings from citizen science" (Stewart et al 2015).

8.7. LONG-TERM DATA

Human harvesting of animals can alter evolutionary processes. For example, catching larger fish encourages maturation at smaller sizes, while trophy hunting for individuals with larger horns, tusks, or antlers can "lead to evolutionary changes in heritable morphological traits that cannot be quickly reversed by natural selection" (Van de Walle et al 2018 p2).

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[38] https://www.dognition.com/.

In populations under pressure from human harvesting of adults, fitness will be optimised by faster life histories (ie: reach maturity and reproduce at an earlier age). But sport hunting regulations in many countries make it illegal to kill females with dependent offspring, as orphaned offspring have a lower survival rate. This produces an artificial selection advantage for "longer periods of mother-offspring associations and slower life histories" (Van de Walle et al 2018 p2).

This is what Van de Walle (2018) found in their analysis of 28 years of data (1987-2015) on brown bears in southern Sweden. The hunting season runs from late August to mid-October for individuals with licenses, and this allows only solitary bears to be killed. All kills are checked by inspectors.

Bears give birth in January, and care for the young until the following spring (mating season) (ie; 1.5 years), or sometimes the spring after that (ie: 2.5 years). In 1987 there were no cases of longer case, but, by 2015, this was around half.

It was calculated that females providing longer care had twice the survival rate of females providing shorter care, but had reduced reproductive opportunities as bears cannot mate when weaning.

Based on standardised data sampling over 27 years in 63 nature protected areas in Germany, Hallmann et al (2017) reported a seasonal decline of three-quarters of flying insect biomass [39]. "Loss of insects is certain to have adverse effects on ecosystem functioning, as insects play a central role in a variety of processes, including pollination, herbivory and detrivory, nutrient cycling and providing a food source for higher trophic levels such as birds, mammals and amphibians. For example, 80% of wild plants are estimated to depend on insects for pollination, while 60% of birds rely on insects as a food source" (Hallmann et al 2017 p1).

In terms of the explanation, Hallmann et al (2017) stated: "We show that this decline is apparent regardless of habitat type, while changes in weather, land use, and habitat characteristics cannot explain this overall decline" (p1).

This study confirmed declines observed in particularly insects (eg: 50% decline in numbers of European grassland butterflies between 1990 and 2011; Van Swaay et al 2013), and in wild vertebrates (eg: over half globally from the 1970s up to 2010s; Ceballos et al 2017).

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[39] This is total weight of those caught as opposed to abundance - ie: number of individuals.

8.8. MUSSELS

Freshwater mussels are filter feeders based at the bottom of lakes, streams and rivers. They trick fish, like the largemouth bass, to nibble at a fleshy lure and the bait "explodes" into a cloud of spawn which latch onto the fish and ride to another area (Bittel 2018).

8.9. DARK DNA

The sand rat (Psammomys obesus) lives in deserts of North Africa and the Middle East, and eats leaves, but doesn't drink water. When kept in laboratories and given a "normal" diet, these rats become obese and develop type 2 diabetes (Hargreaves 2018).

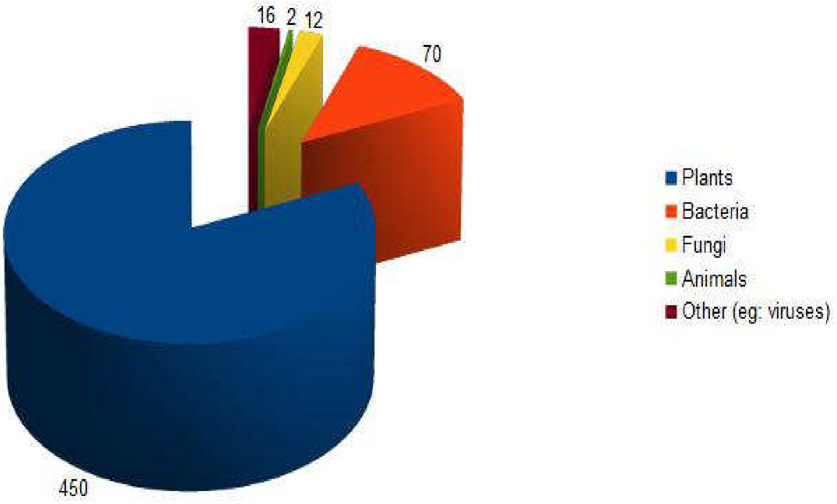
Hargreaves (2018) was interested in why this happened. Research has found that the Pdx1 gene (which is involved in the development of the pancreas and insulin) in sand rats "contains more mutations than any other version of the gene we know in the animal kingdom" (p30).

It has also been found that a large chunk of DNA (nearly 90 genes) is missing from this animal's genome (what has been called "dark DNA").

The sand rat appears to be adaptive for a harsh desert environment, and it may be a product of "mutation-driven evolution" (ie: mutation rates in dark DNA may be so rapid that natural selection cannot act fast enough to remove deleterious variants in the usual way") (Hargreaves 2018).

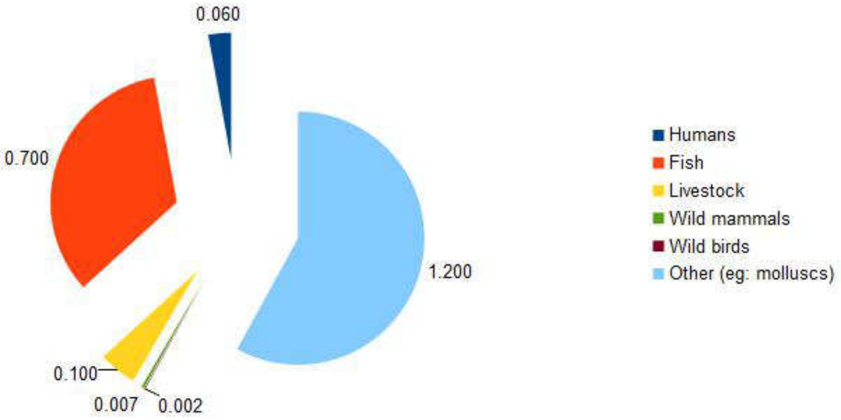
8.10. BIOMASS

Bar-On et al (2018) calculated that the total biomass (weight) of all animals was 2 gigatons of carbon (Gt C) (out of a total of 550 Gt C, mostly plants) (figures 8.3 and 8.4). "Whereas groups like insects dominate in terms of species richness [with about 1 million described species], their relative biomass fraction is miniscule. Some species contribute much more than entire families or even classes. For example, the Antarctic krill species Euphausia superba contributes ≈0.05 Gt C to global biomass, similar to other prominent species such as humans or cows. This value is comparable to the contribution from termites, which contain many species, and far surpasses the biomass of entire vertebrate classes such as birds" (Bar-On et al 2018 p6507).



(Data from Bar-On et al 2018 table 1)

Figure 8.3 - Total biomass of selected groups (Gt C).



(Data from Bar-On et al 2018 table 1)

Figure 8.4 - Total biomass of selected animal groups (Gt C).

8.11. APPENDIX 8A - AGGRESSION

Hashikawa et al (2017) began: "Aggressive behaviour is essential in competing for food, defending the home, protecting self and family, and enhancing overall survival opportunity in both sexes. In many species, mating opportunities are limited and therefore aggression is also used to compete for mates. As a result of natural selection, males in those species often express higher level of aggression. Given that aggressive behaviours are far more prevalent in males in many vertebrates, including humans, most studies of the biological basis of aggression have focused on males" (p1580).

Classic studies of the male brain of rats, for instance, involving lesion and electrical stimulation (eg: Kruk et al 1983) isolated the medial hypothalamus as the biological basis of male aggression. Subsequent studies have found other areas in the hypothalamus are involved (Hashikawa et al 2017).

Gender differences have also been found. Hashikawa et al (2017) reported specific cells in the ventro-medial hypothalamus involved in aggression in female rats. A lactating female will show aggression to an intruder in her home cage, and the cells activated in the brain can be observed using optogenetics (or particularly, fibre photometry). A gene is engineered in the mice to fluoresce when active, and this can be filmed through a transparent area of the skull.

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9. APES AND HUMANS MISCELLANY

9.1. APE ANCESTORS

Ape fossils from past species are rare from the Miocene epoch (23 - 5 million years ago (MYA)). For example, a skull from 7 MYA of Sahelanthropus (an ape that was probably bipedal) has been found (Brunet et al 2002). In the Miocene epoch there was major evolutionary radiation with over forty recognised species from over thirty genera of hominoids (human and ape ancestors) (Nengo et al 2017) [40].

Nengo et al (2017) reported the finding of an infant skull from 13 MYA, which they called Nyanzapithecus alesi. The brain size was estimated to be similar to modern lemurs, and the skull had features similar to gibbons and great apes (Benefit 2017).

The skull also has common features with Oreopithecus, which are "enigmatic and extinct" ancestors (Benefit 2017). "The teeth of Oreopithecus are so unusual that it has been variously described as an ape, an Old World monkey, a primitive ancestor of Old World monkeys and apes, and a member of an extinct lineage unrelated to apes" (Benefit 2017 p161).

Six current species of non-human great apes are recognised (Nater et al 2017):

- 2 orang-utans: Sumatran (Pongo abelii) and Bornean (Pongo pygmaeus);
- 2 gorillas: eastern (Gorilla beringei) and western (Gorilla gorilla);
- Chimpanzees (Pan troglodytes) and bonobos (Pan paniscus) [41].

Nater et al (2017) provided evidence for a third species of orang-utan (Pingo tapanuliensis) in Batang Toru, Sumatra, Indonesia.

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[40] The split between humans and chimpanzees is estimated at 13 - 7 MYA, but the oldest hominin (human ancestor) fossils are 6 MYA (eg: Orrorin; Sahelanthropus) (Barras 2017).

[41] Bonobos were viewed as a sub-species of chimpanzees until the work of Coolidge (1933) showed they are a separate species.

9.2. BRAIN

Brain tissue is expensive to fuel (eg: 1 kg of brain tissue per day requires around 240 kilocalories) (Muchlinski et al 2018). "Despite having relatively larger brains than most non-primate mammals, humans, and non-human primates do not have significantly different overall basal metabolic requirements for their body sizes" (Muchlinski et al 2018 p528). So, how to fuel larger brains?

The "energy trade-off hypothesis" (Wrangham et al 1999) proposed that the increased brain size is balanced by changes in body composition, diet, or behaviour (eg: reduction in the size of the gastrointestinal tract in humans). Muchlinski et al (2018) saw the reduction in skeletal muscle mass as the trade-off. The researchers compared the anatomy of ten species of primates, and found a negative correlation between relative muscle mass and relative brain size.

9.3. SELF-DOMESTICATION

Humans have "domesticated all manner of species for food, hunting, transport, materials, to control pests and to keep as pets. But some say that before we domesticated any of them, we first had to domesticate ourselves" (Barras 2018 p28). The argument is that humans are different to Neanderthals in that "we really may be the puppy dogs to their feral wolves" (Barras 2018).

When a species becomes domesticated, there are physical changes compared to the wild version. For example, a smaller brain - which humans have compared to Neanderthals (Barras 2018).

The change from wild to domesticated species is seen in the "experiment" by Dmitry Belyaev (eg: 1979) (began in 1959) with wild foxes. The most co-operative individuals in a litter were bred over a number of generations. By ten generations, the domesticated version had changes in fur colour and flappier ears, and the male skull had shrunk to look more like that of the female. Smaller teeth and shorter muzzles are also part of the "domestication syndrome" (Barras 2018).

But how does the process of domestication occur? Wrangham (eg: Wilkins et al 2014) proposed the "neural crest hypothesis" which focused on a cluster of cells in the developing embryo called the neural crest. The neural crest is key in the development of the adrenal glands, which are linked to fear and aggression. The breeding of less fearful and less aggressive animals produced smaller adrenal glands at the level of changes to the neural crest. Other observed differences in physical appearance are a byproduct of neural crest changes (Barras 2018).

Boeckx and Benitez-Burraco (eg: 2014) found support in genetic differences between wild and domesticated species, and between humans and Neanderthals that are linked to neural crest development.

But human-domesticated species have a deliberate manipulator, whereas humans do not. The answer is self-domestication, in the sense that early humans benefited from being less aggressive and more co-operative. Sexual selection could have also been involved (Barras 2018).

Hare et al (2012) suggested this process as an explanation for peaceful bonobos evolving from aggressive chimpanzees.

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