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Animal Topics

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CONTENTS

1. ENVIRONMENTAL RISKS

1.1. QUOLLS

Toxic invasive prey are a threat to native predators, as in the case of highly toxic cane toads (Rhinella marina) introduced into Australia in the 1930s (appendix 1A). One native frog-eating predator consequently threatened with extinction is the northern quoll (Dasyurus hallucatus) (figure 1.1), which has no evolutionary history of exposure to such toad toxins (Jolly et al 2018).

In 2003, two toad-free islands in northern Australia were created for northern quolls, while "toad-smart" programmes were introduced. These involved classically conditioning the quolls not to eat cane toads by associating the appearance with an unpleasant (but not lethal) experience. O'Donnell et al (2010) reported that the first programme improved quolls' short-term survival when re-introduced to cane toads.

Subsequently, "toad-smart" trained females survived long-term, and had offspring who did not consume cane toads (Cremona et al 2017). This seemed to be evidence of cultural transmission between mother and offspring. But Jolly et al (2018) pointed out that it was "unclear whether young quolls learnt to avoid toads via cultural learning (by mimicking their mothers), via genetic inheritance of toad avoidance traits from their fathers, or from the ingestion of small non-lethal toads that

(Source: John Gould (1863) "Mammals of Australia volume 1"; in public domain)

Figure 1.1 - Drawing of northern quolls.

induce aversion to live toads" (p140) (appendix 1B).

Jolly et al (2018) introduced a control group into their "toad-smart" training experiments. Twenty-two quolls (half male, half female) were trained with conditioned taste aversion by feeding them a small piece of dead cane toad with a nausea-inducing chemical. This was done until the quolls rejected the food. Seven female quolls were the "toad-naive" control group.

It was established that after training, four the trained quolls and six of the control group died from eating toads in the wild. The average survival time was sixteen days and less than one day respectively. But predation of quolls by dingoes was high, such that the researchers were unable to determine if the offspring of "toad-smart" females also avoided toads, and the control group produced no offspring for comparison.

Overall, Jolly et al (2018) confirmed that "toad-smart" training is effective for the individuals who undergo it.

Conditioned taste aversion has been tried with other animals, including (Tennenhouse 2018):

* Lions killing cattle in Botswana given beef infused with a nauseating toxin.
* Mexican wolves and livestock in North America.
* Steller's jays eating the eggs of the endangered marbled murrelet.

Conditioned taste aversion is best with animals that eat a variety of foods, while single food source animals do not respond (eg: vampire bats) (Tennenhouse 2018) (appendix 1C).

1.2. HUMAN IMPACT ON CULTURE

Cultural behaviour by non-human animals can be defined as "information or behaviour - shared within a community - which is acquired from conspecifics through some form of social learning" (Whitehead and Rendell 2015 quoted in Brakes et al 2019).

Speed of adoption of new behaviours varies between groups of animals, partly due to the inherent propensity of a species. It can lead to sub-populations with distinct behavioural profiles, and increases the importance of key individuals as "repositories of accumulated knowledge" (Brakes et al 2019).

For example, African elephant matriarchs improve the fertility rates of younger females in the group through the transmission of information about the local environment (McComb et al 2001). "Yet, traditional approaches to species conservation often prioritise younger individuals for their direct reproductive potential" (Brakes et al 2019 p1033). Brakes et al (2019) advocated for conservation practices that take account of cultural knowledge among groups of a species.

Chimpanzee communities, for example, vary in certain behaviours (eg: tool use), which show evidence of social learning. These "cultural" behaviours can be inhibited by environmental disturbance. The disturbance hypothesis (van Schaik 2002) sees behaviour transmission as declining with human impact.

Kuhl et al (2019) collected data from the published literature on 144 chimpanzee communities in West and Central Africa, and compared the presence of thirty-one known behaviours based on human impact. Communities located in areas of high human impact showed significantly lower behavioural diversity.

The authors offered four potential mechanisms for the findings:

* Overall less chimpanzees to share behaviours in areas of high human impact.

- Chimpanzees show less numbers of different behaviours as nearby humans increases.

- Effect of climate change on behaviours.

- Habitat degradation reduces opportunities for social learning.

1.3. HUMAN CONTAMINATION

Chemical contaminants can lead to global biodiversity loss (along with habitat loss and climate change). One risk group is pharmaceuticals, particularly psychotropics, like anti-depressants (Whitlock et al 2018).

The anti-depressant "Prozac" (fluoxetine), for example, is widely used in the UK, and studies have found increasing concentrations in wastewater as well as in treated sewage sludge (which is used as agricultural fertiliser). About a quarter of the intake of Prozac is excreted (Whitlock et al 2018). Thus, there is a risk of animals ingesting the substance.

Whitlock et al (2018) investigated experimentally the impact of fluoxetine on 24 wild Eurasian starlings (Sturnus vulgaris). Half of the captured birds were given doses of fluoxetine for 28 weeks equivalent to foraging at wastewater treatment plants (eg: eating earthworms). Courtship behaviours were studied as fluoxetine alters circulating testosterone.

Given a choice of a control or a fluoxetine-dosed female, males sang significantly more to the former and for longer. The males displayed significantly more aggressive behaviours towards the fluoxetine-dosed females than controls. These male behaviours were in response to fluoxetine females being initially more aggressive than controls.

Whitlock et al (2018) summed up: "we have shown that environmental concentrations of fluoxetine can alter courtship interactions in a songbird, with clear effects on male song responses towards fluoxetine-treated females" (p23). In other words, exposure to fluoxetine reduced female attractiveness.

A risk to humans and animals, plastic degrades very slowly to microplastic (MP) particles. Research is finding evidence of MPs in the soil and the atmosphere (eg: Pyrenees; Allen et al 2019). The French mountainous region studied between November 2017 and March 2018 by Allen et al (2019) is sparsely populated, and the MPs found must have been conveyed as atmospheric fall-out. Worryingly, the amount of MPs recorded was comparable to that found in cities (eg: Paris), though the type and shape did differ (Allen et al 2019).

The quantifying of the effects of humans on the biosphere is challenging, and Meineke et al (2018) argued for the use of biological/natural history collections in museums to help. "Natural history collections house vast amounts of data representing diverse taxa in centralised locations... Physical specimens hold data that are of great interest in global change biology, such as nutrients, heavy metals and signatures of pollinator interactions, herbivore interactions, disease and physiological processes" (Meineke et al 2018 p2) [1].

1.4. CLIMATE CHANGE

With climate change producing a more volatile atmosphere, extreme events like heatwaves are expected to be more common, and longer. A heatwave is defined as "conditions when daily thermal maxima exceed the average local maximum by 5 °C for more than five days" (Sales et al 2018). What will be the effect of this situation on animals?

One key effect relates to reproductive sensitivity. For example, male mice exposed to an air temperature of 32 °C for 24 hours had a reduced fertility of 75% (Burfening et al 1970), while male fruit flies cease reproduction above 30 °C (Sales et al 2018).

Sales et al (2018) manipulated the temperature to produce heatwave conditions for red flour beetles (Tribolium castaneum). Individuals were exposed to temperatures that exceeded their optimum (35 °C) by 5 or 7 °C for five days. Males exposed to 42 °C sired half the offspring of those at optimum temperatures, but females were unaffected by temperature.

Sales et al (2018) summarised: "Heatwaves reduce male fertility and sperm competitiveness, and successive heatwaves almost sterilise males. Heatwaves reduce sperm production, viability, and migration through the female. Inseminated sperm in female storage are also damaged by heatwaves. Finally, we discover transgenerational impacts, with reduced reproductive potential and lifespan of offspring when fathered by males, or sperm, that had experienced heatwaves" (p1).

1.4.1. Phenology

A key aspect of climate change impact will be

[1] Rather than describing the current time as the Anthropocene era to cover the impact of humans on the biosphere, Moore (2015) argued that "Capitalocene" was more appropriate.

changes in the timing of biological events (phenology). But it is not easy to disentangle changes related to climate change and those related to natural variations (appendix 1D).

Bell et al (2019) used three different sources of data on insects and birds in the UK to "examine the strength and shape of geographical (latitude, longitude, altitude), temporal (year, season) and habitat (woodland, scrub, grassland etc) variation in phenological rates of change" (p1984).

i) Rothamsted Insect Surveys - Data since 1964 (up to 2010 used) on aerial density of flying aphids from seventeen sites (via suction-traps), and night-flying moths at forty sites (1965 - 2010, using light traps).

ii) UK Butterfly Monitoring Scheme - Counting of butterflies on fixed routes (known as "Pollard walks") at 169 sites (1973 - 2010).

iii) The Nest Record Scheme - Records of nests for thirty bird species at over 11 000 sites (1960 - 2010) [2].

Bell et al (2019) summed up their findings: "We observed a highly–consistent trend towards earlier phenologies for UK bird, moth and butterfly species across habitat types. Though the form of this long–term trend varied among habitats to some extent, there was little evidence that phenological trends were less pronounced in highly structured habitats, such as woodlands, compared to open and exposed habitats such as bare ground and grasslands. Thus, at the relatively coarse scale considered, we found no evidence that complex habitats may be associated with reduced phenological advances and therefore no evidence that species occupying more complex habitats may be buffered against negative impacts of phenological change" (p1988). Put simply, 40-50 years of data showed that seasonal events were occurring earlier now.

1.4.2. Fatal Competition

Samplonius and Both (2019) found that the competition between great tits (Parus major) and pied flycatchers (Ficedula hypoleuca) was affected by climate change in a study of nest boxes between 2007 and 2016. Nine hundred and fifty nest boxes in ten study areas in the Netherlands were observed.

Both species compete for the nest boxes with the

[2] Bird species recognition can have problems (appendix 1E).

great tits being non-migratory and the flycatcher migratory. Each year between early March and late June, regular checks were made of residents and their eggs. Great tits killed 88 flycatchers in the nest boxes.

Climate change could lead to milder winters and more survival of the resident great tit males who defend the nest boxes. The temperature in December correlated with great tit nest-box occupation in the spring. It was found that "great tit density increased after warm winters, and flycatcher mortality was elevated when tit densities were higher" (Samplonius and Both 2019 p327).

1.4.3. Ants' Contribution

Leaf cutter ants (LCA) in Central and South America are "dominant herbivores", and their "foraging and colony construction behaviours relocate plant biomass and excavate soil, altering nutrient distribution and patchiness, and influencing forest structure, under-storey micro-climate and regeneration patterns" (Soper et al 2019 p1). Their concentration of large quantities of organic matter into their colonies, including the colony refuse dumps can produce nitrous oxide (N^2O) hot spots [3], according to work by Soper et al (2019). They measured N^2O levels in lowland tropical rainforests in Costa Rica, which included twenty-two LCA, Atta colombica, colonies in 4 km^2.

The researchers stated: "In most ecosystems, elevated N^2O fluxes are typically episodic and short-lived, characterised as 'hot moments' occurring, for example, during freeze–thaw cycles or re-wetting events. In LCA refuse piles, however, annual temperatures are stable, rainfall persists throughout most of the year, and continuing addition of moist N[nitrogen]-enriched organic material is maintained throughout the diel and annual cycle, and even enhanced (by approximately 30%) during periods of reduced rainfall. In addition, up to one-quarter of Atta colombica colonies relocate annually, and refuse pile sites within colonies are abandoned and relocated nearby at a similar rate. This leads to a high number of abandoned piles on the landscape. Although these piles typically decompose within approximately 1 year, elevated inorganic N concentrations persist in the soil beyond this period, suggesting that abandoned piles could also contribute to additional N^2O production, albeit at unknown rates" (Soper et al 2019 p5).

[3] N^2O is a "greenhouse gas".

1.5. NOISE

The loss or degradation of habitats requires animals to more to new areas. One example is monarch butterflies (Danaus plexippus) moving from agricultural land to roadsides or verges to lay eggs.

Noise is an issue in such habitats, and "despite not having 'ears', there is evidence that some Lepidopteran larvae, like the monarch, can sense and react to loud noise such as passing aircraft" (Davis et al 2018 p2).

Davis et al (2018) performed experiments with monarch caterpillars and simulated road traffic noise. Two rooms were used at a laboratory building in Georgia, USA. The traffic noise room had a minimum of 65 dB as recordings were played to simulate one vehicle passing every 2-3 seconds, while the quiet (control) room had no recordings (maximum 50 dB from outside noise). Larvae were either exposed to noise for two hours (short-term exposure), or one week or 12 days (long-term exposure), and their heart rate was measured.

The short-term (acute) exposure led to an increase in heartbeat frequency of around one-fifth compared to no change in the control group. But there was no differences between the intervention and control groups after long-term (chronic) exposure. The researchers offered three possible explanations for these findings: "(i) that monarch larvae are completely unaffected by long-term road noise, (ii) that they find it stressful but eventually habituate to the noise, or (iii) that insect heart rates simply do not (or cannot) remain elevated during long exposures to a stressor" (Davis et al 2018 p4).

In terms of the second suggestion, studies with birds, for instance, "indicates long-term exposure to stressors leads to weakened physiological stress reactions, which would affect reaction times or performance during real-world stressors. This would be especially damaging for a butterfly that undertakes an arduous two-month trek that is fraught with stressors, including, ironically, avoiding cars on freeways" (Davis et al 2018 p4).

1.6. MISCELLANEOUS

1.6.1. Coat Colour

Mantled howler monkeys (Alouatta palliata) (figure 1.2) have a black coat, but Galvan et al (2019) reported observations of individuals with patches of lighter hair in Costa Rica. In 2013, out of 205 wild monkeys seen, there were twelve observations of patches of light yellowish-cream on limbs and tails, which clearly contrasted with the dark black coat. This was followed up in 2018.

Hair or coat colour is controlled by melanin, which has two forms - eumelanin (responsible for dark brown, grey and black colour) and pheomelanin (responsible for yellow and orange colour). The mix of melanin is genetically determined (Ye 2019).

The changes observed by Galvan et al (2019) are two swift for natural selection, and, anyway, brighter coats would increase the conspicuousness to predators. However, pheomelanin is influenced by sulphur, which these monkeys may have ingested from the environment (ie: sulphurous pesticides in the surrounding plantations) (Ye 2019).

(Source: Leofleck - Leonardo.C.Fleck; leonardofleck@yahoo.com.br)

Figure 1.2 - Mantled howler monkey.

1.6.2. Rewilding

Between 1970 and 2012 there was a 58% global decline in animal populations (ie: amphibians, fish, reptiles, mammals and birds) according to the World Wildlife Fund (Bakker and Svenning 2018). One response to the influence of humans in this decline is "rewilding", which "aims to restore natural processes in ecosystems in general, and often focuses on re-introduction of missing large wildlife species or, in case these went extinct, their proxies" (Bakker and Svenning 2018 p1).

Pettorelli et al (2018) called rewilding "a captivating, controversial, twenty-first century concept to address ecological degradation" (quoted in Bakker and Svenning 2018). The captivating part is the hope of ecosystem restoration, while the "controversial part is that opponents fear that rewilding is the new Pandora's box in conservation and may harm biodiversity, with particular concern about exotic species proliferation as a consequence of rewilding" (Bakker and Svenning 2018 p1).

In terms of studies, Willby et al (2018), for example, reported that beavers increased plant diversity and aquatic beetle abundance. While Derham et al (2018) showed the rewilding native carnivores reduced invasive smaller carnivores.

1.6.3. Freshwater

Freshwater ecosystems provide humans with drinking and irrigation water, food, climate regulation, and recreation, including the populations of freshwater organisms. Increased salt (ie: total concentration of major ions - salinity) can disrupt these ecosystems (ie: salt pollution) (Canedo-Arguelles et al 2019)

Primary salinisation is where natural factors like rainfall, rock weathering, and seawater intrusion affect the freshwater ecosystems. Human activities can accelerate these processes (eg: through construction, mining, agriculture, and rock salt on icy roads), and this is secondary salinisation (Canedo-Arguelles et al 2019).

Canedo-Arguelles et al (2019) highlighted five main questions about freshwater salanisation:

i) What are the main causes? Urbanisation, agriculture, and climate change in studies in the USA and Western Europe.

ii) What are the physiological effects? "Freshwater animals need to maintain an osmotic balance between the ion concentration within their cells and their body fluids, which are strongly influenced by the salinity of the surrounding water owing to body permeability. The maintenance of this balance is key to cellular stability (ie: changes in osmotic pressure can cause cellular damage or death) and requires energy. Freshwater salinisation, through an increase in osmotic pressure, can have drastic effects on the fitness and survival of freshwater organisms" (Canedo-Arguelles et al 2019 p2).

iii) What are the impacts on the ecosystem? Eg: change in breakdown of organic matter by micro-organisms.

iv) Which factors can modify salt toxicity? Eg: other stressors, and the evolutionary context (eg: previous history of salt exposure).

v) How can humans control the process? Eg: regulations; technological solutions.

1.6.4. Life History

Primates have a slow life history (compared to other mammals) which involves a single offspring that matures slowly, a late age of first reproduction, and a relatively long lifespan. This strategy works with high viability (ie: few deaths before reproductive age) (Van Noordwijk et al 2018).

One aspect of a slow life history is long inter-birth intervals(IBIs) (ie: the time between each birth or pregnancy cycle).

Van Noordwijk et al (2018) used the example of orang-utans in Sumatra and Borneo where long-term data were available on particular populations. The estimate of IBI where the first offspring survived until weaning was over 90 months (ie: 7-8 years). Age of first reproduction was around 15 years old, and infant survival until weaning about 90%. Predation by leopards was rare, and starvation was not common.

"The orang-utans' slow life history illustrates what can be achieved if a hominoid bauplan [body plan] is exposed to low unavoidable mortality. Their high survival is likely due to their arboreal and non-gregarious lifestyle, and has allowed them to maintain viable populations, despite living in low productivity habitats. However, their slow life history also implies that orang-utans are highly vulnerable to a catastrophic population crash in the face of drastic habitat change" (Van Noordwijk et al 2018 p38).

1.6.5. Smart Pest Management

Global food production has been, is, and will be a challenge, particularly as 11% of the world is rated as undernourished today (and this is increasing) (Kang 2019).

Global food security is "threatened by harmful organisms—animal pests (insects, mites, nematodes, rodents, etc), microbial pathogens (viruses, bacteria, fungi, chromista) and weeds, collectively termed pests in agriculture" (Kang 2019 p1) (eg: causing 10-30% loss of crop yields annually). Pesticides have been the common response in recent years. But these chemicals have negative effects on humans and non-pest animals. "Abuse of pesticides results in pesticide resistance, biodiversity loss, farmland and environmental pollution" (Kang 2019 p2).

What are the alternatives? One possibility is the use of biotic signalling. This is communication by organisms, and between organisms and plants, "including physical signalling, pheromones, kairomones, hormones, metabolites, peptides, proteins and RNAs" (Kang 2019 p2). So, in other words, controlling pests by manipulating these signals. For example, insects that use vibrational signals to find mates can be prevented by the use of artificial vibrational noise (Polajnar et al 2016). Genetic engineering of crops to be resistant to disease and pests is another technique from a different standpoint (Kang 2019).

1.7. APPENDIX 1A - CANE TOADS

Toxic invasive species like the cane toad can produce "trophic downgrading" - ie: "the disappearance of top consumers, including apex predators" (Doody et al 2015).

Doody et al (2015) found that cane toads were changing the relative densities of predators and prey based on annual surveys in an area of Western Australia between 2009 and 2013. Four predator species (freshwater crocodiles and three species of monitor lizard) and three of their prey species (the Crimson finch, the Gilbert's dragon lizard, and the common tree snake) were surveyed.

Cane toads first arrived in the study area in late 2010, which gave two years of pre-toad data and two years post-toad.

Most notably, two species of the monitor lizards showed statistical significant declines (around a half) after the arrival of cane toads. The Crimson finch showed significant increases (half to three-quarters) in the post-toad period as their predators were killed off.

1.8. APPENDIX 1B - CULTURAL TRANSMISSION

Animal culture is defined as "a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning" (Fragaszy and Perry 2003 quoted in Lamon et al 2017).

Lamon et al (2017) reported an example of this in wild chimpanzees in the Budongo Forest Reserve, Uganda with moss-sponging (or leaf-sponging). This involved using a clump of moss or leaves (or mixture of both) to absorb water in holes, and then squeezing it to drink the water. Observations were made over three years (2014-17).

Originally, eight individuals had shown this behaviour in 2014 (Hobaiter et al 2014). In 2017, five of the initiators were seen still using the behaviour, and forty other individuals .

There were two ways the behaviour could have been transmitted throughout the chimpanzees - vertically (within matrilines - ie: mothers show offspring) or horizontally (between individuals that associate together). The former was supported by experimental observations. "In particular, subjects with a moss-sponger in the matriline were more likely to use a moss-sponge during the experiment than subjects without a moss-sponger in the matriline, whereas moss-spongers were not more strongly associated with other community members displaying moss-sponging from which they could have learned the behaviour" (Lamon et al 2017 p2).

1.9. APPENDIX 1C - DELAYING GRATIFICATION

"Inter-temporal choices" are where "individuals must sometimes forgo their desire for immediate satisfaction to obtain a higher pay-off in the future. Such self-control is considered cognitively challenging because the subjects not only have to suppress impulsive reactions but also must assess and compare the values of different options so as to decide whether or not an immediate option is worth sacrificing" (Krasheninnikova et al 2018 p1).

Delay of gratification tasks offer a small reward now or a higher one later. The length of delay can be varied, or "delayed exchange" can be tested, where the individual is given the low value reward to hold onto and exchange later. Delay maintenance tasks are where an individual can accumulate rewards by resisting them (Krasheninnikova et al 2018).

Delaying gratification has been reported in various species, including chimpanzees, dogs, and sea lions (Krasheninnikova et al 2018).

Krasheninnikova et al (2018) studied parrots, and, in particular 36 individuals from three species of macaws, and African grey parrots hand-reared in Spain. The birds were individually trained to associate different plastic tokens with a highly valued reward (walnut), medium-valued (sunflower seed), and a low-value reward (dry corn).

The parrots were then tested in six choice conditions:

i) Low-value food (LF) vs token for high-value food (HT) - All but one of the tested birds chose the HT above chance level (ie: 15 or more out of 20 trials).

ii) Medium-valued food (MF) vs HT - All birds chose the HT significantly more often.

iii) LF vs token for medium-value food (MT) - The majority of birds chose the MT.

iv) MF vs token for low-value food (LT) - All birds but one chose the MF significantly more often.

v) MF vs MT - Most birds chose the MF.

vi) HF vs HT - The vast majority of birds chose the HF.

All four species of parrots were able to delay gratification when a better reward was offered, but not delay gratification when the future reward was no better. This behaviour was comparable to to chimpanzees in similar experiments (eg: Beran and Evans 2012), for instance (Krasheninnikova et al 2018). However, African grey parrots were poorest.

1.10. APPENDIX 1D - PHENOTYPIC PLASTICITY

Connallon et al (2018) summarised a tension in biology: "Environmental conditions vary across species' ranges, generating selection for locally adapted phenotypes. Nevertheless, gene flow – caused by dispersal and interbreeding between individuals that were born in different regions of the range – opposes genetic differentiation between populations and constrains local adaptation" (p1).

They continued: "Local adaptation hinges upon the balance between the strength of local selection, which promotes population divergence, and the magnitude of gene flow, which erodes it. Weak gene flow allows for strong local adaptation and high genetic differentiation between populations, whereas high gene flow can severely limit such divergence" (Connallon et al 2018 p2).

Phenotypic plasticity is "the ability of an individual genotype to produce different phenotypes in response to the environment. Since plasticity is a property of the individual, it is often hailed as a rapid-response mechanism that will enable organisms to adapt and survive in our rapidly changing world (sometimes termed 'plastic rescue')" (Fox et al 2019 p1). However, plasticity can also be maladaptive.

Plasticity is viewed as important in a species' adaptation to human-induced environmental change. Fox et al (2019) highlighted four broad issues:

i) Plasticity across time - ie: the transgenerational transmission of adaptations. For example, among sticklebacks, Fuxjager et al (2019) found that "parental exposure to elevated water temperature was beneficial for mating success, but only when offspring also developed in the elevated thermal conditions" (Fox et al 2019 p3).

ii) Knowledge of changes in the past in predicting the future - "The ability of species to respond to future environmental change will not be independent of previous environmental experience. Historical conditions impose selection, resulting in the adaptation of populations to the range, average, extreme and/or variation in conditions experienced. Owing to the costs associated with sensing and responding to environmental change via phenotypic plasticity, it is often thought that species that have not experienced environmental fluctuations will have limited capacity to respond phenotypically to future change" (Fox et al 2019 p3).

iii) The role of sexual selection - ie: "adaptation to novel environments matter little if individuals that exhibit plasticity do not mate more often than those that do not" (Fox et al 2019 p4).

For example, among spadefoot toads, females preferred males who sire more plastic offspring, and that male call rates was an honest signal of this ability (Kelly et al 2019).

iv) The "Matthew effect" - "initial advantages lead to further cumulative advantages" (Fox et al 2019 p2).

1.11. APPENDIX 1E - METHODOLOGY

1.11.1. Seeing Rare Birds

Self-identified expert bird-watchers ("birders") are better than novices at identifying species, but they are more likely to misidentify common species as rare or exotic species (Bouillard et al 2019).

This conclusion was based on an online identification test of six common British bird species taken by 2697 individuals. Birder expertise was self-rated from 1 ("novice") to 5 ("experience with most species in Britain (including waders, gulls etc) and abroad (eg: Western Palearctic)").

Overall, self-rated novices correctly identified 35% of the pictures compared to 95% for self-rated experts.

One hundred and thirteen participants misidentified at least one picture as a rare or exotic species for Britain, and these individuals were more likely to be self-rated 4 on expertise ("experience with a wide range of British species, especially common birds").

These findings, Bouillard et al (2019) concluded, have implications for citizen science projects that depend on self-reported data in visual identification of bird species.

1.11.2. Penguins

Adélie penguin (Pygoscelis adeliae) populations are declining in the Western Antarctic Peninsula area, but increasing in the Ross Sea and Eastern Antarctica area. These population patterns may be linked to changes in sea ice extent and concentration, changes in air temperature and precipitation patterns, and thus the prey availability (Borowicz et al 2018).

These observations depend on the accuracy of surveys of penguin numbers. Borowicz et al (2018) described their "novel multi-modal survey" in the Danger Islands (north-western Weddell Sea) area of Antarctica. The survey included:

- Field survey - humans manually counting nests on shore or from photographs.
- Unmanned aerial vehicle images and automated nest detection algorithm.
- Historical aerial imagery (eg: 1957).
- Satellite imagery - eg: guano stained areas.

Overall, the "comparison of available aerial, satellite, and unmanned aerial vehicle (UAV) images suggests that the area occupied by Adélie penguin colonies on the Danger Islands has remained stable or has modestly increased over the last 60 years, though our inference regarding dynamics is unavoidably limited by the lack of imagery between 1957 and 1990" (Borowicz et al 2018 p3).

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2. DEFENCE AND ATTACK

2.1. ANTS

Some ant species have evolved to live in trees either by building their own nests or via myrmecophytes (ie: plants that give ants a nesting place with pre-existing cavities) (Schmidt and Dejean 2018). Group ambushing of insect prey is a key strategy for arboreal ants, but how to stop the prey escaping by flying away, jumping or dropping?

Schmidt and Dejean (2018) described a sophisticated technique used by Azteca brevis ants, who make holes in leaves wide enough for worker's heads. So, "the workers hide, mandibles open, beneath different holes, waiting for arthropod prey to walk by or alight. They seize the extremities of these arthropods and pull backwards, immobilising the prey, which is then spread-eagled and later carved up..." (Schmidt and Dejean 2018 p41). This strategy allowed the ants to capture prey nearly fifty times heavier than itself (eg: winged termites, cockroaches).

The researchers used preliminary observations from Costa Rica and French Guiana before setting up an experiment.

Schmidt and Dejean (2018) observed: "By constructing traps, some arthropods increase the probability of capturing prey, including relatively large or fast-moving ones... Given that a trap permits a predator (and its genes) to act on its environment beyond the limits of its physical capacity (ie: mandibles, beak, mouth, legs), it can be considered an 'extended phenotype' of that predator (Dawkins 1982). Indeed, the quality of these traps, as for bird nests or beaver dams, is correlated with certain alleles of the constructing organisms that are under pressure related to natural selection" (p44).

2.1.1. Social Parasites

Ants face three categories of social parasite (eg: other ant species) (Pullianen et al 2019):

i) Permanent inquilines - Parasites co-exist with the host in their nest.

ii) Slave-makers - Slave-making ants raid other colonies in order to capture and enslave the brood.

iii) Temporary social parasites - This is where "parasite queens invade host colonies, kill the host queen(s), initiate egg-laying, and take advantage of the brood care behaviour of host workers. If successful, this can lead to the loss of the entire future reproductive output of the host colony" (Pullianen et al 2019 p1).

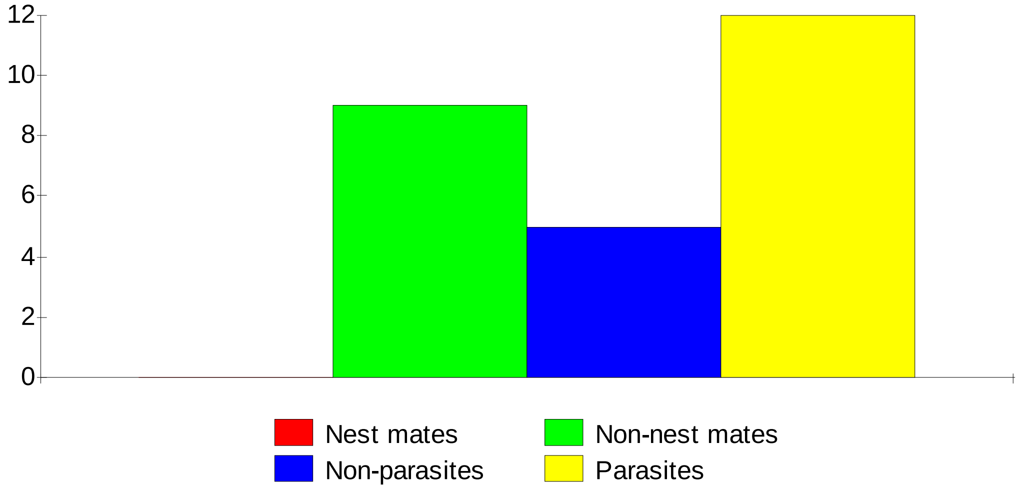
There are evolutionary advantages, then, for hosts to defend against this latter parasite. These include preventing the social parasite queen entering the nest (pre-infection defence), or the ability to distinguish the parasite offspring (post-infection defence) (Pullianen et al 2019).

An example of the latter is the larvae of the host consuming the eggs of the social parasite queen as in the ant Formica fusca. Pullianen et al (2019) studied this experimentally with twenty-eight field-collected colonies in Finland. Host broods were raised in four conditions:

- With nest-mates (control condition).
- With non-nest mates, same species.
- With non-parasites (2 different species).
- With parasites (3 different species).

There was significantly more consumption of the eggs of parasites than in the other conditions (figure 2.1).

"Larvae as a secondary line of defence may, however, not work for species that (unlike Formica fusca) maintain their eggs and larvae separately" (Pullianen et al 2019 p6).



(Nest mates = 0)

(Data from Pullianen et al 2019 table 2 p4)

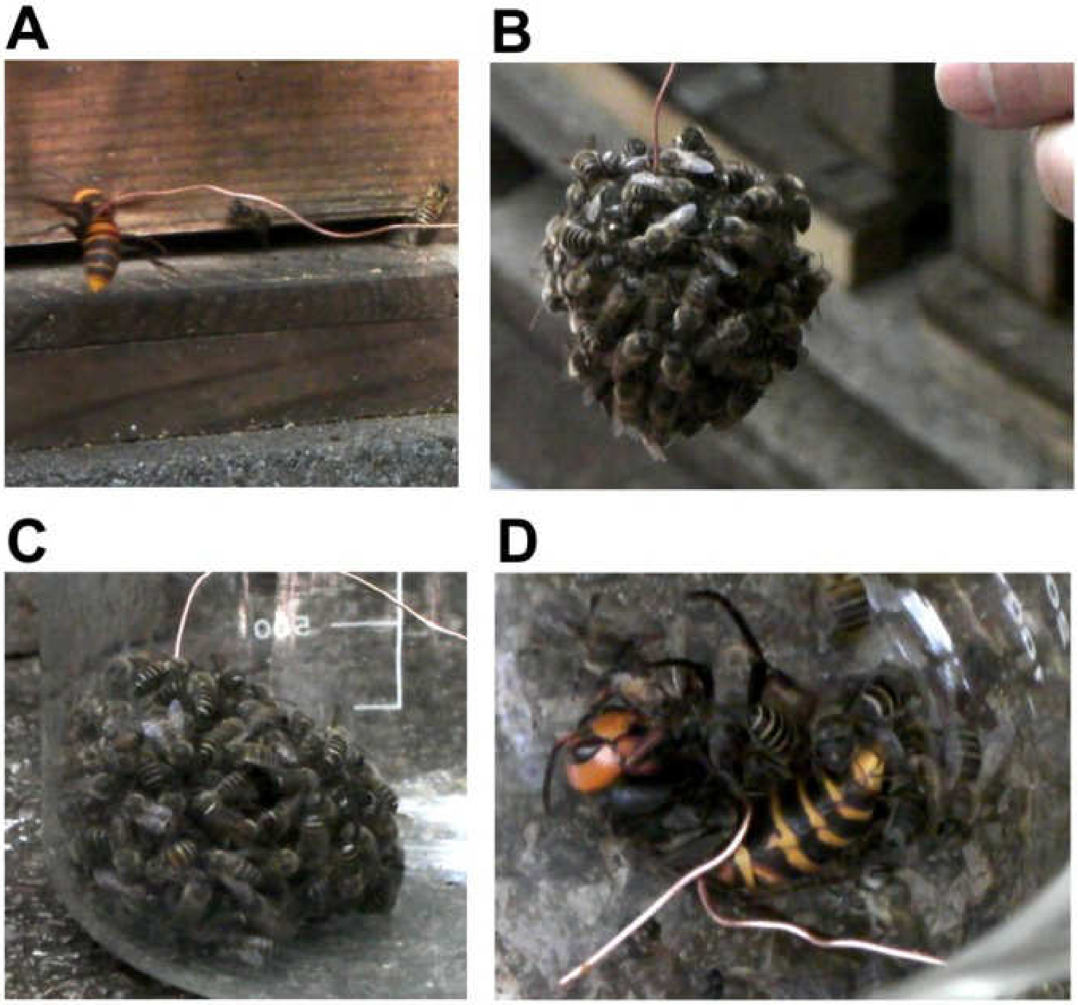
Figure 2.1 - Mean percentage of eggs consumed by larvae of Formica fusca.

2.2. BEE BALLS

One group anti-predator colony defence used by Asian honeybees (Apis cerana) is to surround the much larger giant hornet which is immune to stings. This is the "hot defensive bee ball formation" (Ono et al 1995) where many workers vibrate their flight muscles, which produces heat up to 46°C for up to ten minutes to kill the hornet (Yamaguchi et al 2018).

The honeybees also suffer a cost for this behaviour - reduced life expectancy. Yamaguchi et al (2018) studied this behaviour experimentally with honeybee colonies in Japan. The "bee ball formation" was elicited by presenting a hornet on a wire to the bees (figure 2.2). The bees who participated in "bee ball" subsequently lived for significantly less time than the non-participants.

It was also found that individuals who participated in one "bee ball" were more likely to participate in subsequent ones, and to be at the centre of it.



A - Hornet placed on wire.
B - "Bee ball" forms around hornet.
C - "Bee ball" placed in glass beaker.
D - Hornet on wire found to be dead after "bee ball" removed.

(Source: Kiya et al 2012 figure 5 p15503; https://www.researchgate.net/figure/Artificial-hot-defensive-bee-ball-formation-A-hot-defensive-bee-ball-is-usually-formed_fig5_235740127 ; CC BY 3.0)

Figure 2.2 - Creation of "bee ball" and collection of participants in study with similar methodology to Yamaguchi et al (2018).

2.3. COCKROACHES

The emerald jewel wasp (Ampulex compressa) is a parasitoid insect who stings the brain of the American cockroach (Periplaneta americana) and creates a "zombie". "When the venom takes effect, the cockroach becomes passive and can be led by its antenna into a hole, where the wasp deposits an egg and then seals the exit with debris. The cockroach has the ability to walk, run, or fly if properly stimulated, but it does not try to escape as it is slowly eaten alive by the developing wasp larva" (Catania 2018 p32).

Thus the venom does not entirely paralyse the cockroach, rather there is a "long-lasting pacification", a loss of free will, and "hence is often referred to as a 'zombie'" (Catania 2018 p33).

This strategy evolved because the cockroach is too large to be moved by the wasp if completely paralysed, but large enough to be a good food source for the developing larva. The wasp, however, must sting the cockroach through the soft tissue of the neck and directly into the brain rather into the body fluid as with other wasps.

Keasar et al (2006) described ten stages in the attack that takes about one hour in total, from host targeting, thorax sting (first sting paralyses front legs), and head sting to host insertion into the nest, and oviposition (depositing eggs in body of cockroach).

The cockroach can employ defensive behaviours which may even kill the wasp. Catania (2018) filmed the wasp-cockroach interaction in the laboratory to study this behaviour.

In 28 of 55 trials, cockroaches made no defence and were stung within three minutes [4]. In the other half of trials, six defensive strategies were observed:

a) Stilt-standing (an "on-guard" position) - standing as tall as possible on all legs to keep the vulnerable neck area away from the crawling wasp. Two-thirds of cockroaches who used this defence avoided being stung in three minutes.

b) Kicking with hind legs - "The movement was reminiscent of a baseball bat swing, in that it required a wind-up phase, a swing phase, and considerable follow-through with the entire body of the cockroach" (Catania 2018 p37).

c) Contact-triggered escape response.

d) Escape response when grasped by wasp.

e) Raking, stabbing, and "stiff-arm" defence with leg spines - The use of the spiny legs in a raking movement to dislodge a wasp or pierce the soft tissue of the wasp's abdomen.

f) Biting - Used after first sting when legs paralysed.

[4] "For the purposes of this study, a time period of 3 min without a successful first sting was chosen to be scored as a successful defence, based on the premise that an uncontained, and unstung, cockroach in nature would eventually escape, particularly in cases during which the wasp gave up stalking for long intervals" (Catania 2018 p44).

2.4. AVOIDANCE

One general defence strategy is to avoid predators. This can be done by moving to a predator-free area or one with a lower density of predators ("safe habitats"), or by changing their daily activity patterns (ie: forage when predators absent).

Detecting predators indirectly (ie: without meeting them) is done via odours, as in the faeces and urine of carnivore predators. The odour will be different if the same prey species has been eaten as compared to another species. These odours are called kairomones - "semio-chemicals emitted by an organism that benefit another species" (Prada et al 2018).

Prada et al (2018) investigated kairomones at four study sites in Spain with the European rabbit (Oryctolagus cuniculus) and its predator, ferrets (Mustula putorious furo). Ferret scat was left at the sites manipulated in one of three ways - rabbit in the diet ("treatment-rabbit"), beef in the diet ("treatment-beef"), or water odour (control). The presence of rabbits over nine days was measured by the amount of droppings.

Significantly less rabbit droppings were counted in treatment-rabbit areas than the other two (figure 2.3). This suggested that rabbits recognised their own species' scent in the ferrets' scat, and consequently avoided the area.

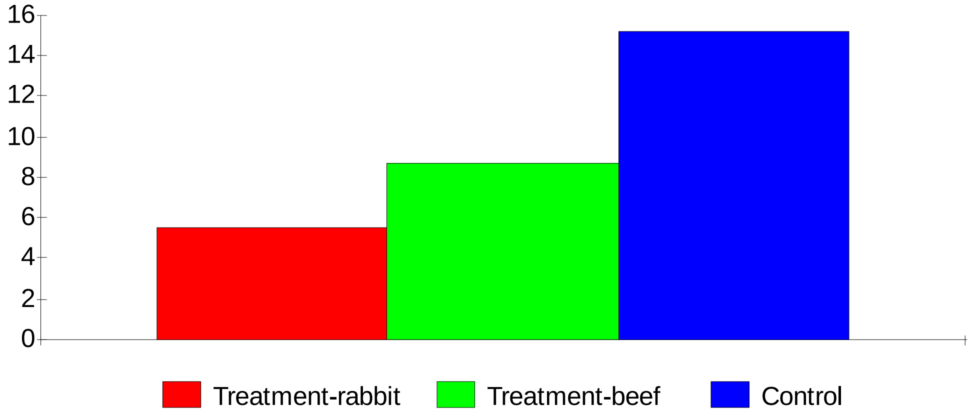


Figure 2.3 - Mean rabbit droppings per 1 m².

2.5. AUTOTHYSIS

Social insects like ants, termites, and aphids, can use self-destructive defence behaviours called autothysis, "self-explosion" or "suicidal bombing", where individuals kill themselves to defend the colony (Kutsukake et al 2019).

Kutsukake et al (2019) described a particular example of this behaviour by soldier nymphs of the social aphid Nipponaphis monzeni. When the plant-made nest (gall) is damaged by intruders, "soldier nymphs erupt to discharge a large amount of body fluid, mix the secretion with their legs, and skilfully plaster it over the plant injury. Dozens of soldiers come out, erupt, mix, and plaster, and the gall breach is promptly sealed with the coagulated body fluid" (Kutsukake et al 2019 p8950). This behaviour is self-sacrificing as the soldier nymphs die.

Kutsukake et al (2019) found that the body fluid of soldier nymphs had evolved to allow a "super- or hyper-clotting body fluid" to be used to seal the gall breach. It was an adaptation of the individual immune system, such that the researchers referred to this as an example of "social immunity". This is "the mechanisms in social animals to combat against pathogens, parasites, and other enemies to ensure survival of their society as a whole" (Kutsukake et al 2019 p8950).

2.6. HYPER-ACCUMULATION

Hyper-accumulation is a defence strategy where a plant or animal stores an elevated concentration of a noxious chemical in its body which deters eating by predators. For example, a type of fern (Chinese brake) in the USA hyper-accumulates arsenic from the soil, and Florida fern caterpillars (Callopistria floridensis) (figure 2.4) take on the high concentration of arsenic through eating the fern (Jaffe et al 2019).

(Source: Chazz Hesselein)

Figure 2.4 - Florida fern caterpillars.

When give a choice of two ferns with different levels of arsenic, the caterpillars preferred lower levels of arsenic, which could be ingested without being fatal. The Florida fern caterpillar appears to be "the only known terrestrial animal capable of accumulating arsenic, and may have developed novel physiological and behavioural adaptations to regulate the negative effects of arsenic" (Jaffe et al 2019 p480).

This caterpillar gains functional advantages from the arsenic ingestion, particularly in the form of decreased predation and parasitism (Jaffe et al 2019).

2.7. PREY HANDLING AND DEFENCE

Prey handling is a term used to describe the process after capturing the prey, which involves subduing, killing and consuming. This is particularly important when the prey is larger than the predator as in the vertebrate prey of a bird called the loggerhead shrike (Lanius ludovicianus mearnsi) (figure 2.5).

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

Figure 2.5 - Loggerhead shrike.

Sustaita et al (2018) filmed the prey attacks of 37 shrikes at San Diego Zoo Institute for Conservation Research. Vertebrate prey included mice and lizards, which were immobilised and killed by "repeatedly biting the head or neck, or by latching onto the nape with their beaks and vigorously shaking them with rapid, long-axis head rolls" (Sustaita et al 2018 p2). The shaking movements caused damage to the prey's spinal column. It was estimated that "a peak instantaneous acceleration corresponding to 6 g for a mouse’s body about its neck while being shaken by a shrike. By analogy, victims of low-speed rear-end car crashes experience head accelerations of 2–12 g" (Sustaita et al 2018 p3).

Other research has reported how shrikes impale their prey on thorns in the wild (Sustaita et al 2018).

2.7.1. Velvet Ants

Gall et al (2018) observed that predation is "an extremely powerful selective force driving the evolution of morphology, physiology, and behaviour among animals... Because of the intense nature of the interaction (prey either escape to live another day or die), it has resulted in a bewildering array of defensive structures and strategies to mitigate this risk" (p5852).

These researchers concentrated on velvet ants (figure 2.6) (parasitic flightless wasps) that lay eggs on ant or bee pupae. Defensive strategies include a venomous sting [5] and bright coloration to advertise itself as well as warning squeaks and smells (appendix 2A). Furthermore, the exoskeleton is exceptionally strong.

Gall et al (2018) studied these defence strategies experimentally using velvet ants from eastern and western USA (eg: Dasymutilia vesta).

a) Mockingbirds that visited a feeding station were offered dead or live velvet ants. They preferred other food to the dead ants, and avoided the feeder when live ants present.

b) A mole, after being stung by the velvet ant, retreated from other velvet ants.

c) Four shrews bite ants, but rejected them after being stung. The exoskeletons appeared to survive the bites.

d) Two toads from two different species initially swallowed a velvet ant, but regurgitated it, and subsequently avoided velvet ants.

[5] Starr (1985) developed a pain scale for humans to rate stings received from insects. The scale varied from 0 ("no pain") to 4 ("traumatically painful"). One species of velvet ant was rated at 3.

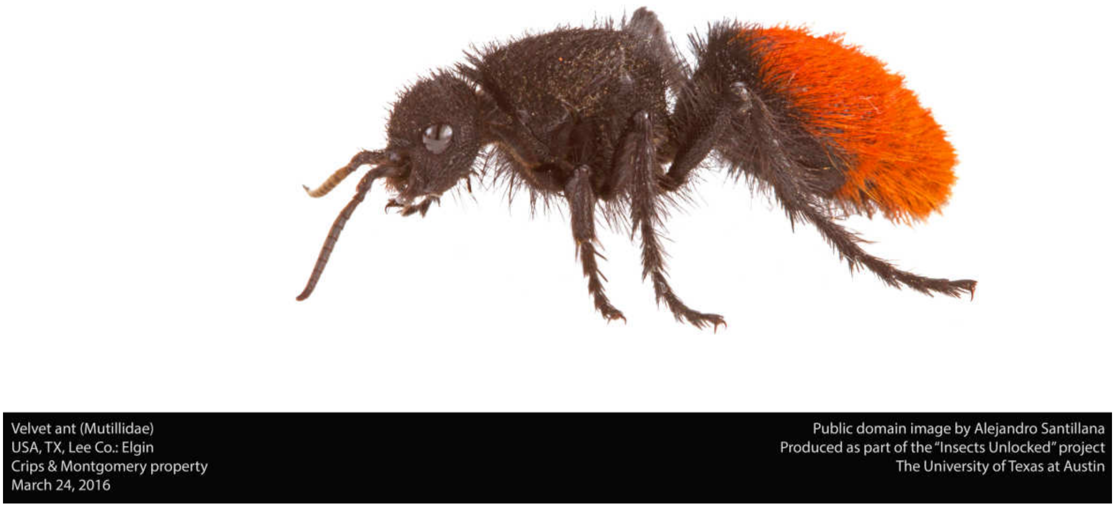


Figure 2.6 - Velvet ant.

e) Lizards - after initial contact, velvet ants were avoided.

Gall et al (2018) concluded: "The results of this study indicate that velvet ants from both the Eastern and Western United States possess a myriad of defences that render them almost invulnerable to a suite of potential predators including amphibians, reptiles, birds, and small mammals" (p5859).

2.8. CONTRA-HIERARCHICAL AGGRESSION

Among social species, dominance hierarchies reduce conflict between group members. But contra-hierarchical aggression (CHA) (ie: subordinates aggressive towards dominant individuals) does occur sometimes.

Seil et al (2017) outlined three aspects of CHA: "(1) it is a prerequisite and early marker of instability in dominance relationships, rank reversals, or social upheaval; (2) it is a way subordinate females may increase their social status and thus their fitness, and; (3) in despotic [6] and nepotistic [7] species it

[6] Despotic hierarchies are where dominant individuals enforce their position with serious injury for transgressors.

involves greater risk of severe retaliation by the dominant and her kin" (p559).

Seil et al (2017) investigated CHA among over 350 female rhesus macaques in captivity in California. Groups were observed for around 200 hours by four observers, of which two at a time recorded aggressive, submissive, and status interactions using event sampling.

CHA was influenced by intrinsic factors, like the weight/size of the individuals, age, and the extrinsic factor of social support. So, "having many non-kin allies increases the likelihood of initiating insubordinate aggression, whereas kin allies appear to be more important for protecting against insubordination" (Seil et al 2017 pp568-569). CHA was greater when the subordinate individual was older than the dominant one (highest for 8 vs 22 years old) (compared to vice versa), and where the subordinate individual was heavier/larger than the dominant macaque (highest when 7 kg difference).

Seil et al (2017) concluded that "despite a rigid and despotic social environment, rhesus macaque females do not passively accept their inherited social status, but rather are dynamic agents who appear to consistently monitor and test the relationships that limit their fitness, and integrate complex information to determine whether to defer to or rebel against the impositions of dominant group members" (p570).

2.9. MISCELLANEOUS

2.9.1. Chemical Weapons

Marine cone snails use chemical weapons injected into captured fish prey (eg: venoms called conotoxins). One species, the geography cone (Conus geographus) (figure 2.7) is different in both chemical weapon and hunting technique. This predatory cone snail releases a specialised toxin called the "nirvana cabal" (Olivera 2002) into the water to "stun" the nearby prey fish, and then engulfs them before a venom injection (Safavi-Hemami et al 2015).

The nirvana cabal contains specialised insulins which produce hypoglycaemic shock in the prey (ie: lowers blood glucose levels and reduces locomotor activity) (Safavi-Hemami et al 2015).

[7] In nepotistic hierarchies rank is inherited from close kin.

(Source: Kerry Matz, US National Institute of General Medical Services; in public domain)

Figure 2.7 - Geography cone snail

2.9.2. Visual Lure

Conspicuous body coloration can function to attract females, warn predators, or lure prey. In the latter case, a visual lure has been reported in snakes like the sidewinder rattlesnake, and some frogs and toads [8], mimicking food or a potential mate (Zhang et al 2015).

Brightly coloured body parts as a visual lure has also been found among some web-building spiders to increase the web interception rate of insects (eg: Bush et al 2008; appendix 2B).

Zhang et al (2015) reported the case of the brown huntsman spider (Heteropoda venatoria) which lures insects close enough to jump and snatch from the air. This spider has a moustache-like white stripe across the forehead region of its brown body.

The researchers made 63 cardboard dummy spiders with white stripes and without, which were left at sites at a university in Taiwan. Video recordings were made of the approaches made by flying insects to within 5 cm of a dummy. The white-striped dummies attracted significantly more flying insects.

Then live spiders with their white stripes shaved off were compared to unchanged spiders, and they attracted significantly less flying insects. So, the white stripe attracts prey, but "it remains unclear why

[8] Eg: Hagman and Shine (2008) cane toad (appendix 2C).

the white stripe of the brown huntsman spider is visually attractive to nocturnal moths" (Zhang et al 2015 p123).

2.9.3. Zebra Stripes

Explanations for a zebra's stripes include to stay cool on hot days (less credible) to "dazzle camouflage" against predators (Marshall 2019) (table 2.1).

Hypothesis	Evidence Against
Camouflage Confusion of predators	African lions take zebra prey disproportionately more than expected (Caro et al 2019).
Social benefits	No differences between striped and unstriped equids in patterns of association, say (Caro et al 2019).
Heat regulation	Controlled experiments show no benefits in keeping cool in the African sun (Caro et al 2019).

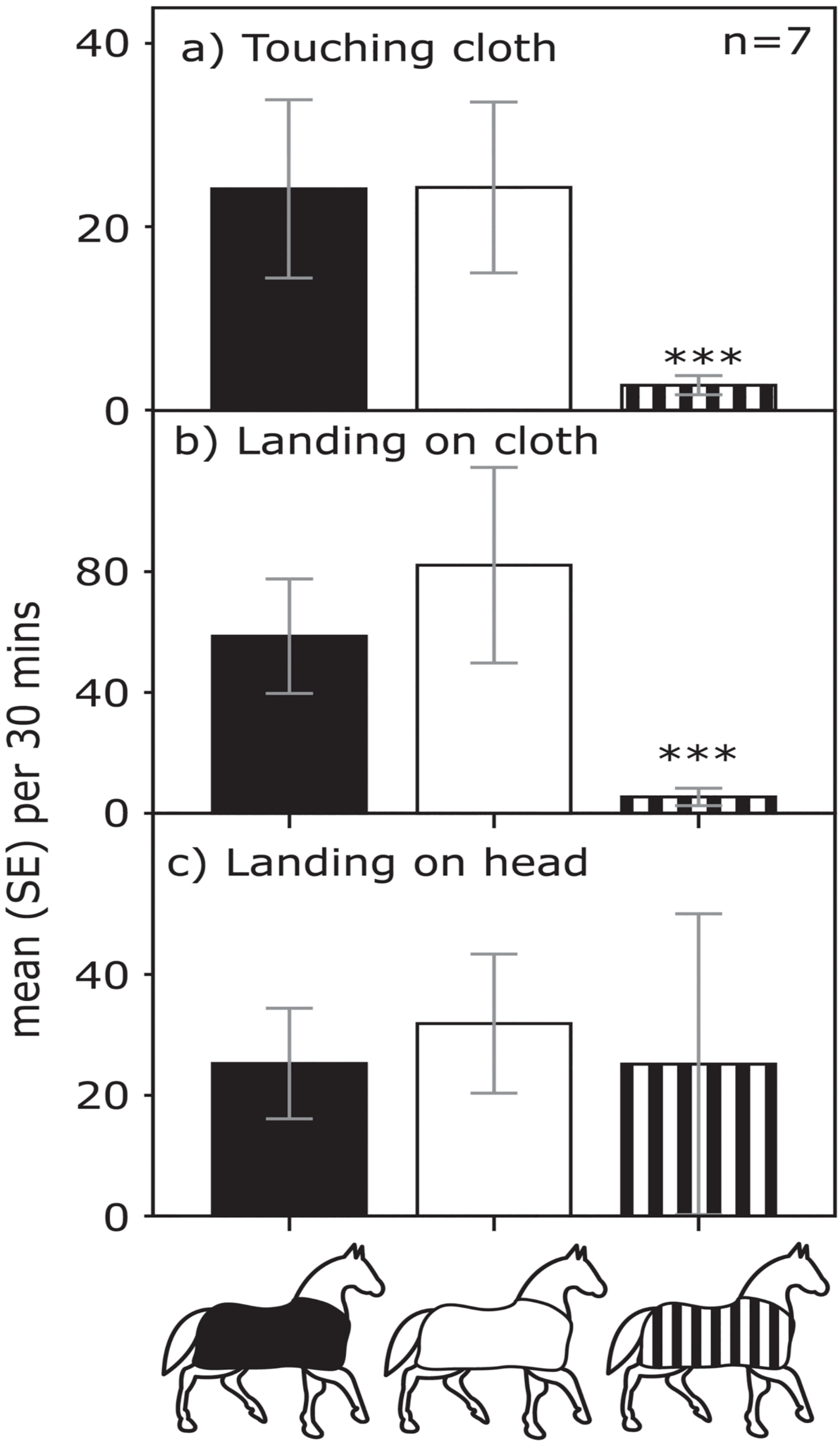
Table 2.1 - Selection of hypotheses for the zebra's stripes.

Caro et al (2019) tested the idea that the stripes confuse blood-sucking horse flies, which are a constant hazard, by putting striped coats on horses in the UK.

Initially, Caro et al (2019) observed three zebras and nine horses kept in captivity in the UK. The number of wild tabanid horse flies landing on each animal were recorded in five-minute observation periods. Though the same number of flies circled both sets of animals, significantly fewer flies landed on zebras than on horses.

In the experimental part of the study, three cloth coats were placed on seven horses for 30-minute periods. One coat was black, one was white, and the other was black and white striped. Significantly fewer flies landed on the horses wearing the striped coat (figure 2.8).

The researchers also video-recorded flight behaviour of the flies close to the captive animals as well as the behaviour of the equids in response to the flies. In the former case, Caro et al (2019) commented: "Focusing to the 0.5 s period prior to actually contacting equids' coats, we noticed that tabanids approaching zebras failed to decelerate in a controlled fashion towards the end of their flight trajectories whereas they steadily decelerated before landing or touching horse pelage... Moreover, flies often simply bumped into zebras but fail to land or fly away..." (p7).



(Source: Caro et al 2019 figure 2)

Figure 2.8 - Mean number of flies (a) touching, landing on (b) cloth coat and (c) uncovered head based on cloth coat worn by horse.

In terms of the equid's behaviour, the zebras showed behaviours (eg: tail-flicks) which reduced the time the flies spent on their body.

"In summary, multiple lines of evidence indicate that stripes prevent effective landing by tabanids once they are in the vicinity of the host but did not prevent them approaching from a distance. In addition, zebras appear to use behavioural means to prevent tabanids spending time on them through constant tail swishing and even running away. As a consequence of both of these morphological and behavioural defences, very few tabanids are able to probe for a zebra blood meal..." (Caro et al 2019 p11).

2.10. APPENDIX 2A - BRAZEN PREY

Warnings by "brazen prey" include the bright colours of poison dart frogs (with toxins in skin), odours produced by sea slugs (with stingers), and ultrasound warnings to bats by foul-tasting tiger moths (Leavell et al 2018).

Leavell et al (2018) focused on bioluminescent fireflies (Photinus pyralis), which are noxious to bats. Fireflies were presented to big brown bats (Eptesicus fuscus) in one of three conditions:

- Free-flying and flashing.
- Free-flying and non-flashing. The bioluminescence areas of the body were painted over with black or red paint.
- Tethered and flashing.

Controls included free-flying wax moths and scarab beetles. The experiments took place in large dark rooms over four nights. All eight naive bats caught a firefly on the first night, but subsequently avoided them. Leavell et al (2018) observed: "Over just a few nights, the bats in our experiment learned to avoid these chemically protected animals" (p1).

The bats learned quickest in the free-flying and flashing condition, which suggested the use of visual and echolocation information together by the bats (ie: multi-sensory integration).

2.11. APPENDIX 2B - BUSH ET AL (2008)

Bush et al (2008) tested whether the yellow and white bands on the wasp spider (Argiope bruennichi) (figure 2.9) attracted prey in three experimental conditions. On webs spiders were placed where the bands were painted black ("blacked out" condition) (n = 45), the spider was hidden by a leaf ("leaf-shielded" condition) (n = 45), or "naturally coloured" (control) (n = 70). The number of prey captured over six days was measured.

The naturally coloured spiders captured significantly more prey than the other two conditions. "This result supports the hypothesis that bright coloration in wasp spiders attracts insect prey. This hypothesis is consistent with the general expectation that the colour yellow is perceived by prey insects as similar to certain food resources such as flowers, new leaves or plant growth" (Bush et al 2008 p1340).

(Source: Evanherk)

Figure 2.9 - Female Argiope bruennichi.

2.12. APPENDIX 2C - HAGMAN AND SHINE (2008)

Hagman and Shine (2008) studied toe waving as a lure by cane toads (Chaunus marinus). This involved rapid vertical movement of the longest (middle) toe of the hindfoot, and it attracted other toads. Note that the cane toad can cannibalistic.

Experiments used live toads and a "toe-simulator" (an engine that rotated a metal and rubber arm). Other toads, but not crickets, were attracted to the toe waving (real or artificial). "The demonstration that edible-sized (metamorphic) toads approach toe waving adult conspecifics (but not otherwise identical adults not engaged in toe waving) provides direct evidence of a fitness advantage to this behaviour" (Hagman and Shine 2008 pp127-128).

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3. MOVEMENT

3.1. LEARNING MIGRATION

Migration by ungulates (hooved mammals) appears to be based on social learning and memory. For example, adult white-tailed deer follow the movement patterns that their mothers did (Jesmer et al 2018).

The direction and location of movement are the behaviours that are learned. Jesmer et al (2018) used the model of bighorn sheep (Ovis canadensis) (figure 3.1) in the American West translocated to vacant land. It was predicted that "if migration does not stem primarily from a genetically inherited suite of traits, individuals should fail to migrate when first translocated into novel landscapes where migration would be a profitable strategy" (Jesmer et al 2018 p1023). GPS collars were affixed to 80 translocated sheep and 129 individuals that were part of populations that had lived in the same area for over twenty years. "Whereas individuals from historical populations were largely migratory [65-100% of individual], translocated individuals initially were not [less than 10%]. After multiple decades, however, translocated populations gained knowledge about surfing green waves of forage (tracking plant phenology) and increased their propensity to migrate" (Jesmer et al 2018 p1023). This was confirmed by additional data on individuals from five populations of moose (Alces alces).

Jesmer et al (2018) argued that "ungulates accumulate knowledge of local phenological patterns over time via the 'ratcheting effect', wherein each generation augments culturally transmitted information with information gained from their own experience, a process known as cumulative cultural evolution. Cultural transmission therefore acts as a second (non-genetic) inheritance system for ungulates, shaping their foraging and migratory behaviour and ultimately providing the primary mechanism by which their migrations have evolved" (p1024).

(Source: John Sullivan; in public domain)

Figure 3.1 - Rocky Mountain bighorn sheep.

3.2. NOT MOVING

The geographical range of a species is the area that is inhabited, and depends upon factors like food availability, climate, and the presence of competitive species. The latter may cause a species to be mobile, while limited dispersal ability may restrict a species to stay put (Bladon et al 2019).

Bladon et al (2019) considered the role of temperature in restricting the range of a species, in the case of a bird, the Ethiopian Bush-crow (Zavattariornis stresemanni). It is limited to 7800 km^2 in southern Ethiopia. Compared to two other bird species in the area, "Bush-crows began to pant and moved to the shade at significantly lower temperatures than did either of the less temperature-restricted starling species. This suggests that Bush-crows are physiologically more influenced by high temperature than the two starlings, and therefore that they start to feel physiological stress at lower temperatures" (Bladon et al 2019 p555). Put simply, the Bush-crows do not extend their range because they cannot cope with higher temperatures in the warmer months in the surrounding areas.

Panting is the means that these birds reduce body heat as they do not sweat. Observations by the researchers led to estimates that at over 40° C, the Bush-crows spent over half their time panting (compared to half of that time in the other species). The Bush-crows were observed in 100 watches from 5-10 m away, and the White-Crowned starlings in 30 watches, and the Superb starlings in fifty watches. Each watch lasted 4-5 minutes on average.

It was also observed that the food intake rate (ie: items per minute) of the Bush-crows declined with increasing temperatures, but not so in the other species.

3.3. MISCELLANEOUS

3.3.1. Lunar Cycles and Oysters

Marine organisms respond to lunar cycles as well as tidal ones. The Pacific oyster (Crassostrea gigas) has been well studied here.

There is a daily rhythm, a circannual clock, and "a strong tidal rhythm, modulated by neap-spring tidal (semi-lunar) and anomalistic Moon cycles (Payton and Tran 2019 p1).

Payton and Tran (2019) investigated their lunar rhythm in Arcachon Bay, France, by measuring the daily valve opening amplitude (daily VOA) five days around each new moon, full moon, and first and quarter moons (between December 2014 and April 2015).

Daily VOA was greatest during the new moon phase, and varied the rest of the month, which suggested that oysters were "able to sense moonlight despite its extremely low intensity compared with sunlight... [and] that oysters can detect if the moonlight is increasing or decreasing" (Payton and Tran 2019 p3). Whether this lunar-related behaviour was internally or externally regulated, the researchers could not say (Payton and Tran 2019).

3.3.2. Oophagy

The development of ultrasound technology, primarily its portability, has allowed the observation of pregnant females of live-bearing elasmobranchs (sharks, skates, and rays). Tomita et al (2019) reported the use of underwater ultrasound with three captive tawny nurse sharks (Nebrius ferrugineus) in Japan (figure 3.2). The divers went to 10-metre depth and placed the equipment near the pelvic fin for around five minutes.

The interesting finding was that the embryos actively swam between the right and left uterus, "which is contradictory to the 'sedentary' mammalian foetus" (p122), and "which is the first reliable evidence for active embryonic locomotion of viviparous vertebrates" (Tomita et al 2019 p124).

The reason for this behaviour, Tomita et al (2019) hypothesised, is the unique reproductive strategy of these sharks called oophagy. The embryo does not receive nutrients from its egg yolk nor from a placenta, but by eating unfertilised eggs (nutritive eggs) in the uteri. "It seems likely that in this mode of reproduction, the active swimming ability of the embryo may allow it to effectively search and capture nutritive eggs in the uterine environment" (Tomita et al 2019 p124).

Also it was observed that "the cervix of the tawny nurse shark sometimes opens, and the embryo exposes its head out of the uterus through the cervix. This phenomenon is in contrast to that seen in mammals where the cervix is tightly closed until birth" (Tomita et al 2019 p124).

Locomotion in the uterus, brief exposure to the external environment, and feeding on eggs (ie: chewing) all prepare the sharks for post-natal life and reduce the risks of death (Tomita et al 2019).

(Source: OATz; Free Art License)

Figure 3.2 - Baby nurse shark.

3.3.3. Aerobic Push-Ups

Smooth softshell turtles (Apalone mutica) overwinter underwater by partially burying themselves in sand and mud. Plummer and O'Neal (2019) video-recorded twelve individuals in an outdoor pool in Arkansas and ten juveniles in a laboratory cold room.

"Overwintering individuals were responsive to physical stimulation. Turtles moved around on the pool bottom and reburied themselves during the course of the winter but did not rise to the surface to obtain air" (Plummer and O'Neal 2019 p28). Interestingly, the turtles showed a "push-up" behaviour, which the researchers believed had a ventilating function as dissolved oxygen in the water is "breathed" through the skin (cutaneous respiration). The turtles increased the frequency of push-ups in warmer water (with a lower percentage of oxygen), and in experimentally manipulated low-dissolved oxygen-water (Plummer and O'Neal 2019).

3.3.4. Place of First Mating

Commonly performed behaviours can occur in the same or different places. In the same place reduces search costs, and the risk of uncertainty if the behaviour has been successful before (eg: feeding). For example, the natal environment can influence adult habitat preference and increase performance as the individual is used to that type of environment.

But environments change, and so plasticity is important. Learning by experience, however, requires a longer lifespan to collect the knowledge. In short-lived animals, innate behavioural responses have some flexibility for learning by experience (eg: moths and butterflies) (Proffit et al 2015).

These plant-feeding (phytophagous) insects experience different plants and past experience is part of future preferences. Proffit et al (2015) showed this with the Egyptian cotton leafworm moth (Spodoptera littoralis) and plant preference for mating (ie: plant of first copulation influences plant choice in subsequent copulations).

In the basic experiment, male and female moths mated for the first time on cabbage, cotton, or no plant. Subsequently, when given a choice, individuals preferred to mate on the plant type of the first mating, "whereas exposure to the plant alone or plant together with sex pheromone does not affect this preference" (Proffit et al 2015 p365).

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4. COMMUNICATION

4.1. HORMONAL COMMUNICATION

Naked mole-rats (Heterocephalus glaber) are unusual among mammals in being eusocial. One female, the queen, is reproductively active, with a limited number of males (eg: 1-3). "Subordinates exhibit no mating behaviour but provide coordinated support during foraging, colony defence, and care of the queen's offspring (alloparenting)" (Watarai et al 2018 p9264).

The alloparenting behaviours include licking, grooming, and weaning the pups, and this caring behaviour is usually performed in response to increased progesterone and oestrogen. Watarai et al (2018) hypothesised that the subordinate females, who have small ovaries, "might acquire hormones, like progesterone and oestrogen, from external sources, such as the ingestion of the queen's faeces" (p9264).

Experiments were performed with naked mole-rats bred at two Japanese universities. The first experiment tested whether the female subordinates showed alloparenting activity at a constant rate. Seven individuals' reaction to pup vocalisations were measured during three points of the queen's reproductive cycle (gestation, post-partum, and non-lactation). Given a choice of tunnels between a recording of pup vocalisations and no sound [9], the female subordinates responded to the pup vocalisations only during the post-partum period (ie: after birth - when alloparenting is required).

The second experiment fed five female subordinates pellets of faeces from a pregnant or non-pregnant queen for ten days [10]. The pup vocalisation choice test was then performed. Response to the pups was displayed after

[9] Response to the five minutes of pup vocalisations was measured in three ways:

- Speed of response to vocalisation (latency);
- Duration of stay in area of vocalisations;
- Duration of exploration for source of vocalisations.

[10] Naked mole-rats "routinely perform coprophagy (appendix 4A). As a means of maximising limited resources, naked mole-rats often consume faeces and induce other individuals, including the queen, to excrete faeces" (Watarai et al 2018 p9264).

eating the pregnant queen's faeces.

The last experiment gave five female subordinates faeces from a non-pregnant queen with oestrogen added or not for ten days. The females responded to the pup vocalisations more than controls.

In other eusocial species, the dominant individuals release pheromones to control subordinate behaviour. But this would not work with naked mole-rats because the smell organs are not well developed, and the tunnels where they live are well ventilated (Watarai et al 2018).

"Thus, naked mole-rats may have evolved a unique means of communication that does not rely on the use of volatile or non-volatile odorants, but rather on a hormone. Using hormones instead of pheromones for communication may directly mediate the reproductive state and behaviour of another individual. It is also interesting that this communication occurs through coprophagy, a habit that might have evolved as an adaptive strategy to maximise the use of resources under harsh semi-desert conditions. It might be difficult for a single queen to distribute her faeces to all members of the colony. However, some subordinates consistently remain in the nest, and the queen remains in the nest with increasing frequency during the gestation period. Thus, it is plausible that the nearby subordinates eat faeces from the pregnant queen and become alloparents. Coprophagy near to the nest of the queen is enough to induce co-operation between a queen and subordinates for the growing pups" (Watarai et al 2018 p9268).

Critics have questioned whether the queen could produce enough waste to feed the entire colony. Chris Faulkes said, rather graphically, "It'd have to be coming out like machine gun fire" (quoted in Whyte 2018).

4.2. MEERKATS

Group-living animals receive social information from other members, like the presence of a predator. But such information could be inaccurate, irrelevant, or even deceptive.

Rauber and Manser (2018) investigated how individuals assess the sentinel calls in a meerkat (Suricata suricatta) colony in the Kalahari Desert, South Africa. Sentinel calls were recorded from sixty-six individuals. The researchers then played back recordings of the "calming call" (ie: no predators) (n = 544), and the foraging behaviour of colony members was observed.

Individuals foraging spent less time being vigilant in response to more experienced sentinels ("super guards") (based on more frequent sentinel behaviour in the last three months as scored by observers) compared to "rare sentinels" (2.1% vs 5.1% of foraging time scanning the surroundings). Individuals were also significantly less vigilant in response to sentinel calming calls of littermates compared to other group members.

Rauber and Manser (2018) summed up: "Our study on meerkats shows that foraging group members discriminate between the calming calls of different sentinel individuals and adjust their personal vigilance behaviour accordingly. In particular, we found that foraging test subjects showed the lowest personal vigilance when hearing social information of individuals that acted as sentinel most often, and littermates. Dominance status, sex and age, however, did not have a significant influence on the observed vigilance levels" (p2).

This suggests that meerkats must have the cognitive abilities to keep track of the experience of individuals as sentinels (Rauber and Manser 2018).

Schibler and Manser (2007), for example, found that meerkats did not discriminate between individuals giving aerial alarm calls - ie: the response was the same to all individuals. The cost of ignoring alarm calls is higher than calming calls, as there is some flexibility with the latter (Rauber and Manser 2018).

4.3. HORSES

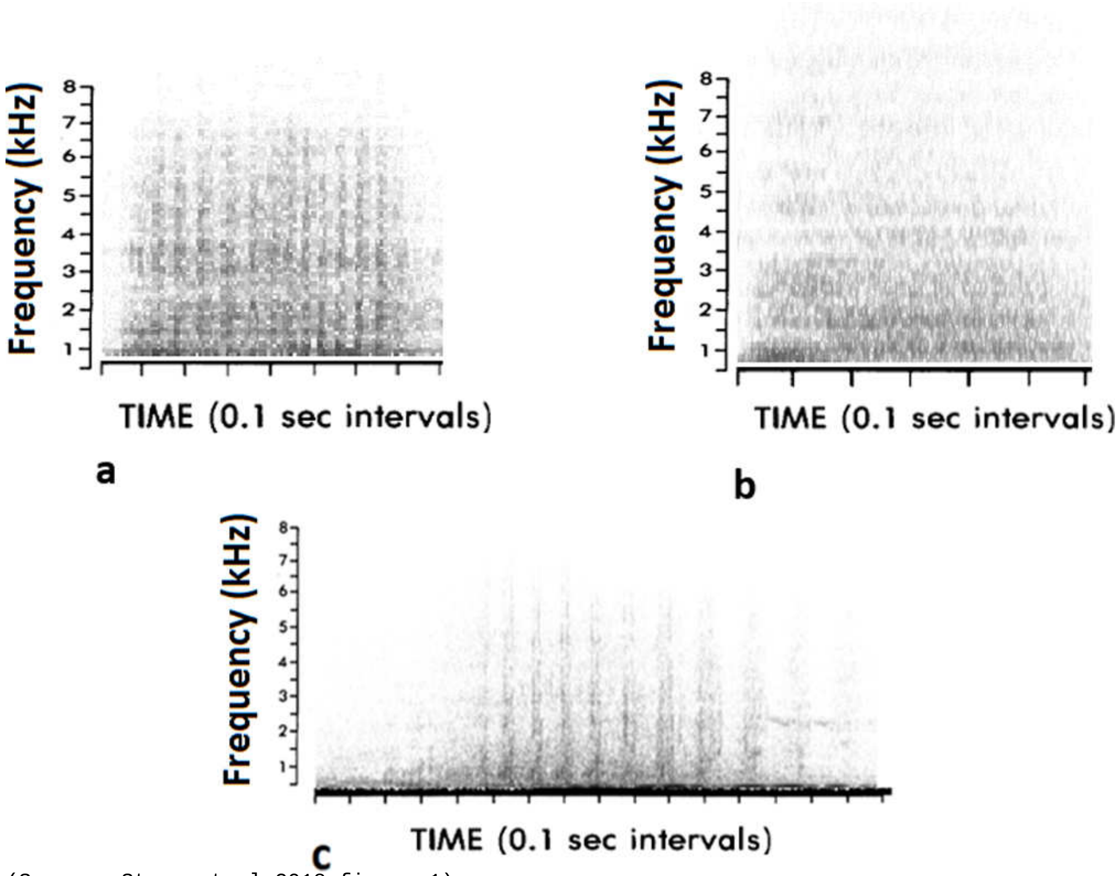
Important for the welfare of captive/domesticated animals, like horses, is the ability to assess their positive emotions. Physiological measures, like heart rate, for example, are not always reliable. "Heart rate frequency increases during food anticipation (a supposed positive condition), but decreases during a grooming simulation (interpreted as a relaxing positive event) in horses..." (Stomp et al 2018 p2). Furthermore, behavioural signs can be ambiguous (eg: yawning) (Stomp et al 2018).

Stomp et al (2018) noted three non-vocal sounds produced by horses (figure 4.1):

- Snore - "a very short raspy inhalation sound produced in a low alert context, such investigating a novel object or obstacle".

- Blow - "a short very intense non-pulsed exhalation through the nostrils and is generally associated with vigilance/alarm postures (eg: presence of a fear-inducing object in the surroundings)".

- Snort - "a more or less pulsed sound produced by nostril vibrations while expulsing with air, with a slightly longer duration in comparison to the blow" (pp3-4).

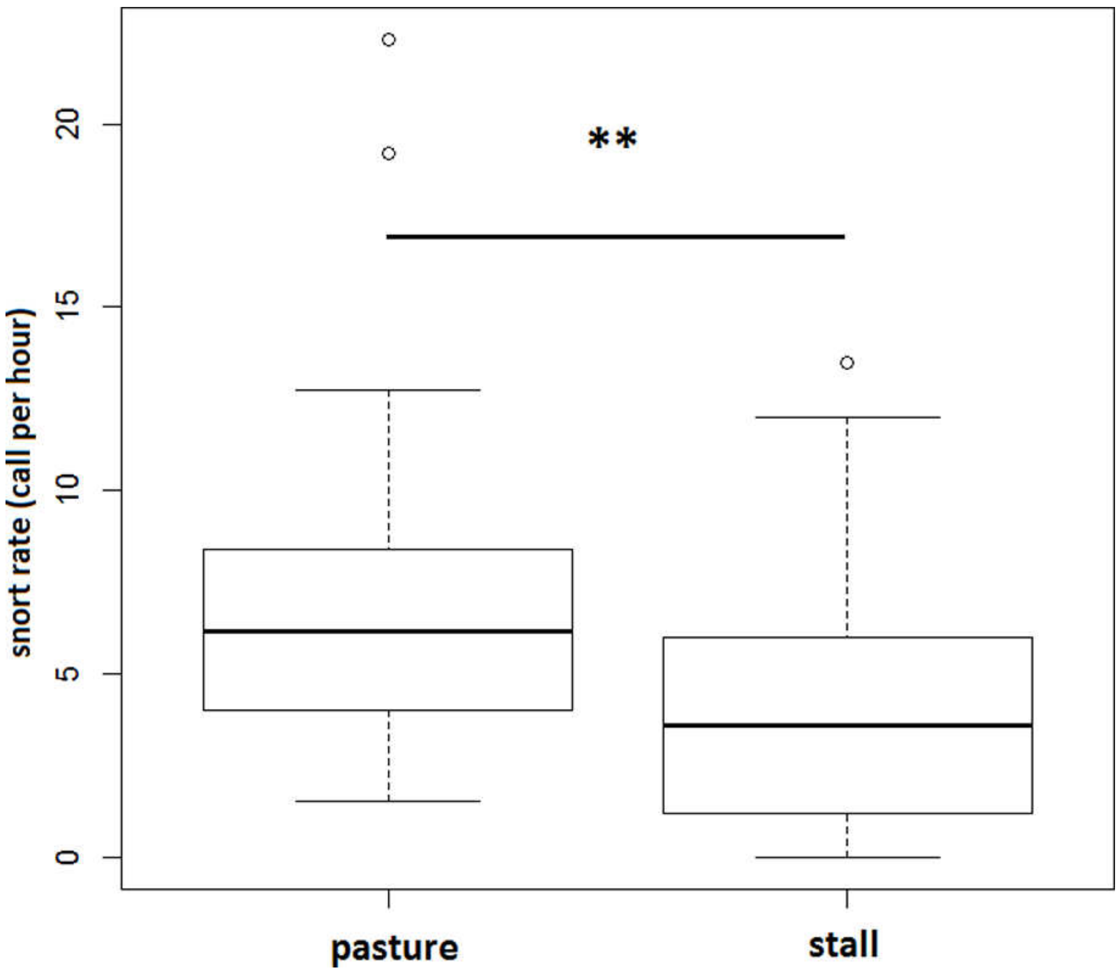


(Source: Stomp et al 2018 figure 1)

Figure 4.1 - Spectrogram of (a) a snore, (b) a blow, and (c) a snort.

Stomp et al (2018) focused on snorts in 48 horses studied at four sites (stables at riding schools and in fields/pasture) in France. The snort rates of each horse were measured in different situations (eg: approaching horse in stall or fields). In total, 560 snorts were recorded.

Many snorts were produced by horses in fields, and while eating (figure 4.2). The frequency of snorts was negatively correlated with stress score (as measured by aggressive response, for example). The findings "provide a potential important tool as snorts appear as a possible reliable indicator of positive emotions which could help identify situations appreciated by horses" (Stomp et al 2018 p15). The snort may be seen as a sign of contentment as in cat purring.



(** = significant difference between means - p = 0.004)

(Source: Stomp et al 2018 figure 3)

Figure 4.2 - Snort rate in two different situations.

4.4. ORANG-UTANS

Non-human communication can be highly sophisticated, but it usually lacks "displaced reference" - ie: "the capacity to transmit information about 'things that are remote in space or time (or both)'" [Hockett 1960] (Lameira and Call 2018 p1).

However, Lameira and Call (2018) provided evidence of this ability in the communication between orang-utan mothers and infants. Seven wild females in Sumatra, Indonesia, were presented with four models - "a human experimenter walking on all fours along the forest floor draped over with a sheet with one of four different types of print: tiger patterned [a natural predator historically known to predate on orang-utans at this site, colour patterned (abstract pattern), white with multi-coloured spots, and plain white" (Lameira and Call 2018 p5). Each individual was exposed to a different model for two minutes each day. The vocalisations of the mother were recorded.

The mothers did not give an immediate alarm call, which would have been risky with real predators, but called on average seven minutes later.

The researchers explained that "if mothers fully suppressed their vocal alarm responses, then the infant would unlikely have the opportunity to ever learn from safety that such an encounter was dangerous. Vocal displacement seems to be therefore the result of a balance by the mother between minimising the risk of detection by the predator on the one hand and providing information to their infant about predation on the other hand" (Lameira and Call 2018 p3).

This behaviour showed evidence of higher-order cognition in the displaced reference, which van Schaik et al (2013) also reported in wild flanged orang-utan males, who "advertise future travel direction one day in advance through long calls that facilitate associations with females" (Lameira and Call 2018 p4) [11].

4.5. MISCELLANEOUS

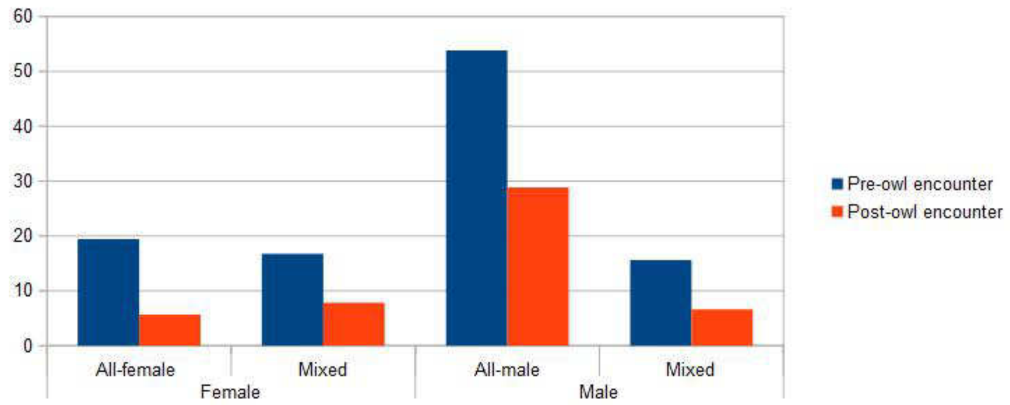
Eilam et al (2012) reported research with social voles (Microtus socialis) on anxiety and predators. Twenty-five female and 38 male voles were kept in all-male, all-female, or mixed gender groups, and their cage was placed in the centre of a barn-owl (main predator) aviary. Food was placed on the roof of the cage, such that "when the owls swooped down on the vole cage to feed, they threatened the voles but could not reach them through the wire-mesh" (Eilam et al 2012 p961). The cages were left over night in the aviary. The anxiety level of individual voles was tested before and after the owl encounter using the open-field test. The animal is left in the middle of an open area and their movement is measured. More time in the open area (ie: away from the walls) is taken as less anxiety.

All voles showed significantly less time in the open area after the owl encounter than before it (figure 4.3). There were differences, however, depending on the group in the cage. In the mixed gender groups, which mirrored the normal social group, "all females and some males displayed high anxiety, while other males displayed low anxiety" (Eilam et al 2012 p964). Eilam et al (2012) explained the behaviour of the latter males thus: "we suggest that these were individuals of high social rank and that the response of these individuals reflects the natural division of labour in social voles" (p964) (ie: these males have a protective role and take more risks).

[11] Other sophisticated behaviours have been observed in orang-utans (appendix 4B).

In the male-only groups, all individuals displayed high levels of anxiety, while "females in the all-female groups revealed higher anxiety levels that females grouped with males" (Eilam et al 2012 p966).

Eilam et al (2012) summed up: "the present results indicate that the more natural group structure of both females and males was better able to cope with stressful events, with some of the males performing their protective role, being less anxious compared with individuals in the same-gender groups" (p966).



(Data from Eilam et al 2012 table 1 p962)

Figure 4.3 - Mean time (seconds) spent in open area based on group.

4.6. APPENDIX 4A - CAECOTROPHY

Rabbits produce two kinds of faeces - hard (nutrient-poor) and soft (contains protein and vitamins) - and they often consume the latter. Stopping this behaviour experimentally reduced the growth of young rabbits (Wang et al 2018).

The eating of own faeces for nutritional purposes is caecotrophy. Wang et al (2018) explained the behaviour: "Many small herbivores have a natural instinct of caecotrophy. Because of the small body shape and their digestive tract volume is limited, the average residence time of food in the digestive tract is relatively short. In order to meet their nutrition needs, small herbivores need to obtain adequate high-quality food. Small herbivores mainly rely on low-quality, high-fibre plant stems and leaves as food
sources, with cellulose from symbiotic micro-organisms in the hind-gut aiding in digestion. Because microbial fermentation takes longer time than the average residence time of food in the digestive tract, increasing digestibility by ingesting incompletely-digested

nutrients is an important nutritional strategy for small herbivores".

4.7. APPENDIX 4B - ORANG-UTAN SELF-MEDICATION

Animals have been observed to use minerals, plant parts, or anthropods as self-medication for parasites, ailments, and skin infections. These are ingested or anointed on the fur or skin ("fur-rubbing") (Morrogh-Bernard et al 2017).

For example, fur-rubbing with a foam created by chewing a particular leaf was observed in Bornean orang-utans in Indonesia (Morrogh-Bernard 2008). Subsequently, the plant (Cantley's dracaena) was analysed chemically and found to have anti-inflammatory properties. This fits with "the hypothesis that fur-rubbing is a form of self-medication used to treat joint and muscle inflammation" (Morrogh-Bernard et al 2017 p3).

Adult females were nine of the ten observed cases of this behaviour, and it "may be the extra weight added by carrying offspring for females when climbing, and may also explain why they concentrate mainly on their arms when fur-rubbing. The fact that local people use the crushed leaves for sore muscles and joints further supports the concept that orang-utans would use it to treat similar problems" (Morrogh-Bernard et al 2017 p4).

In terms of ingestion, chimpanzees chew certain leaves to produce a bitter juice which is swallowed to combat intestinal parasites (eg: Huffman and Seifu 1989).

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5. FACES AND RECOGNITION

5.1. HORSES

Humans remember the facial expressions of specific individuals, and this is beneficial for social bonding and aggression avoidance. What about other animals? Proops et al (2018) tested horses.

Forty-eight horses at equestrian centres in Southern England were tested in one of two conditions. The horses were familiar with human interactions. The horses were individually shown a large photograph of "female 1" (F1) expressing a happy or angry facial expression for two minutes. Then 3-6 hours later the horse was exposed to a woman showing a neutral expression - F1 in the experimental condition, or "female 2" (F2) in the mismatched control condition. The behaviour of the horse was recorded, including gaze, approach or avoidance, stress behaviours, and heart rate measures. The live females did not know which photographs the horses had previously seen.

Horses have been found to have a left gaze bias (and right hemisphere processing) for negative and potentially threatening stimuli, and a right gaze bias (and left hemisphere processing) for positive stimuli (Proops et al 2018).

Proops et al (2018) explained the expectations of the researchers: "If horses remember a single brief exposure to an emotional facial expression of a particular individual, then we would expect the experimental group to react either positively or negatively to the neutral model based on which facial expression they had previously seen, but the mismatch control group not to differ in response" (p1428).

The main finding was that there was a significant left gaze bias towards F1 after the negative photograph (mean 18 seconds compared to 4 seconds after happy photograph), and significantly more time viewing with the right eye F1 after the positive photograph (mean 7 seconds vs 1 second after angry photograph). The mismatch control group showed no difference in eye gaze after either photograph (average of 10 seconds viewing F2).

Proops et al (2018) summed up: "Our results provide clear evidence that some non-human animals can effectively eavesdrop on the emotional state cues that humans reveal on a moment-to-moment basis, using their memory of these to guide future interactions with particular individuals" (p1428).

5.2. GOATS

Pitcher et al (2017) used a cross-modal preference looking paradigm to investigate auditory-visual recognition by goats (Capra hircus) of individuals of their own species. Domesticated goats in England were played the call of an individual while presented with two goats in neighbouring pens. It was predicted that the goats would look at one goat faster and for longer if they recognised the call.

In series one, the choice of goats was a stablemate (ie: familiar) or a random herd mate (unfamiliar), and two different calls of the stablemate or the unfamilar goat were played.

The goats looked significantly faster and for longer at the congruent goat (ie: matched with call) than the incongruent one for both the familiar and unfamiliar individual.

In series two, the choice was between two unfamiliar goats, and, in this case, there was no difference in looking between the congruent and incongruent individual.

In conclusion, "goats are capable of cross-modal recognition of familiar social partners" (Pitcher et al 2017 p7).

The researchers tried to control for side bias by varying the position of the two goats, but not for olfactory cues.

The findings also need consideration because, as Pitcher et al (2017) noted, "goats did not show an association between calls and visual cues for other, less familiar herd members, it is difficult to determine if what we observed is class recognition (stablemate versus other) or individual recognition mediated by familiarity and the opportunity to learn other individuals' unique traits" (p8).

Proops and McComb (2012) used the same method with horses and the voices a familiar or unfamiliar handler. The horses did not look towards unfamiliar humans when presented with their voice. Pitcher et al (2017) observed that "this might indicate an inability to infer that an unknown voice originates from an unknown individual. Alternatively, they suggest that individuals might not be motivated to respond to a stranger" (p9). This point is relevant to the study with goats.

5.3. CONSPECIFICS

Male facial masculinity is linked to attractiveness to females in primates (eg: humans, capuchins, macaques) (Rosenfield et al 2019).

For example, Rosenfield et al (2019) presented female rhesus macaques with a choice of two male macaque faces, and measured the time spent looking at one as a preference (known as the look-time paradigm). The masculinity of the faces was scored based on eight features (eg: nose length, jaw width). For example, male macaques have significantly wider jaws than females.

One hundred and sixty-seven free-roaming females on the island of Cayo Santiago (near Puerto Rico) were each tested once (but only data from 107 trials were usable). In each case, a photograph of a masculine and a feminine face were presented.

There was no significant difference in the amount of time looking at each face, but the female macaques "did look longer at the masculine than the feminine image in a significantly higher proportion of trials than expected by chance (looked longer at masculine image: 64 trials; looked longer at feminine image: 41 trials; 2 ties...) (p6). In trials where there was a high difference in masculinity between the two faces, the participants looked significantly longer at the masculinity faces, but there was no difference in the low-difference trials.

Rosenfield et al (2019) summed up: "The finding that females distributed their visual attention unevenly between masculine and feminine faces indicates that the variation in facial masculinity we measured was not only perceived by, but also salient to, female rhesus macaques. It is possible that variation in facial masculinity has no reliable connection to underlying physiological, behavioural or genetic factors in male rhesus macaques, in which case there may be no fitness repercussions of female attention to such variation. However, as male facial masculinity is related to hormone levels and behaviour in humans and other primates..., it seems likely that females’ ability to discriminate variation in this trait is the result of evolutionary processes" (p8).

5.4. EXACT FACIAL MIMICRY

"Exact facial mimicry" is the matching of facial expressions by two individuals in a social interaction. It is a common behaviour in humans, but rare in other species (eg: gorilla; Palagi et al 2019) (Taylor et al 2019).

Taylor et al (2019) reported evidence of it among captive Malaysian sun bears (Helarctos malayanus) (figure 5.1) in Malaysia. Video-recordings of social play were

(Source: Kenpei)

Figure 5.1 - A Malaysian sun bear in a zoo.

made in 2016 and 2017.

The "open-mouth face" was the focus of the observations. Thirteen bears showed an open-mouth face within one second following the open-mouth face of a playmate during face-to-face social play. The open-mouth face was produced significantly more often in response to an open-mouth face than to a closed mouth of a playmate. There was no relationship between facial behaviour and play duration. Overall, these findings suggested that a degree of social sensitivity among these animals (Taylor et al 2019).

5.5. SELF

The ability to recognise oneself in the mirror is viewed as evidence of self-awareness. A few non-human species (eg: chimpanzees, bonobos, orang-utans, Eurasian magpies) show the behaviour as measured by the "face-mark test". A mark is surreptitiously applied to an animal's forehead as it sits in front of a mirror. An attempt to remove the spot is taken as a sign of self-awareness (Deleniv 2018).

Self awareness is viewed traditionally as a sign of mental complexity. Alternatively, if the brain is a model-building machine for the world, self-awareness goes with awareness of others' minds in social species. In non-social species, self-awareness is thus not required. This means that "self-awareness is not higher-order, or intrinsically more complicated, than consciousness... It is another example of consciousness" (Michael Graziano quoted in Deleniv 2018).

A recent addition to the "mirror self-awareness club" is rhesus macaques, which Chang et al (2017) showed could be learned. These animals can use the mirror to find hidden objects, and this ability can be adapted into passing the face-mark test. Chang et al (2017) trained three young male rhesus monkeys in this way.

These individuals were trained to touch a red laser pointer light in the mirror to gain a food reward. In time "the monkey has learned the association between the light spot image in the mirror and the corresponding position on his face" (Chang et al 2017 p3259). Then the face-mark test was performed without food reward. "During the dye mark test, the monkeys exhibited typical mirror self-recognition behaviours, including face or ear mark touching, followed by looking and/or smelling at their fingers..." (Chang et al 2017 p3260). Subsequently, trained individuals left with a mirror examined themselves spontaneously in the mirror which suggested mirror self recognition (table 5.1).

• Genital-related behaviours - eg: "First looking at the mirror, and then raising a leg to examine his own genital area".

• Genital-unrelated behaviours - eg: "Looking at the mirror and touching his own face, head, or teeth, or pulling his own face or head hair, and then looking at or smelling at his fingers".

(Source: Chang et al 2017 table 1 p3261)

Table 5.1 - Examples of spontaneous mirror-induced self recognition behaviours of trained rhesus monkeys.

5.5.1. Cleaner wrasse and mirror

Kohda et al (2018) reported that cleaner wrasse fish (Labroides dimidiatus) showed the three stages of mirror self-recognition:

i) Social reactions towards the reflection - eg: initially aggressive response as towards a rival.

ii) Idiosyncratic behaviours towards the mirror - 5 of them include "upside-down approach".

iii) Frequent observation of their reflection - more time spent in non-aggressive postures close to the mirror.

Ten wild fish were presented with a mirror in their individual tanks, and the responses were video-recorded eight times over a two-week period.

Because fish lack hands to touch the mark in the mark test as in mammal studies, behaviour to remove irritants or ectoparasites from the skin surface (ie: glancing or scraping) were used as the response measure. Kohda et al (2018) commented: "When we marked fish with brown-pigmented elastomer on the lateral body surfaces in locations that could be viewed directly, the fish increased scraping behaviour of the mark sites, indicating they regard the colour dots as ectoparasites to be removed".

But Gordon Gallop suggested that the wrasses mistook the marks for parasites on the skin of other fish (quoted in Ye 2018).

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6. EVOLUTION AND MATING

6.1. OLDER MALES

Female choice of an older male has both advantages and disadvantages. In reference to the latter, germ-line mutations accumulate over a male's life and these can reduce fertility and offspring viability. On the other hand, survival to an older age is a signal of good genetic quality (an inheritable trait). "These two opposing selection pressures will act simultaneously, with the expectation being that female preferences will reflect the balance between costs and benefits of mating with older or younger males" (Rodriguez-Munoz et al 2019 p1).

Female age choice works in species where there is a high variance in date of birth in males (eg: birds, mammals, reptiles). But choosing older males is not straightforward with seasonal species (ie: all males born simultaneously), then there will be no age differences. With annual species, males are born in a short time window, which does allow for some age variation. "Females could delay mating in order to sample only old males, but they risk dying and deteriorating in the meantime and they would have to delay producing offspring. Furthermore, delaying mating would select for males that emerge later, which might reduce the power of delaying mating as a strategy to select for longer-lived adult males" (Rodriguez-Munoz et al 2019 p2).

Rodriguez-Munoz et al (2019) reported on female choice in the cricket Gryllus campestris with twelve years of observational and genetic data from a meadow in northern Spain. These crickets are a single annual generation, and adult age is the result of variation in date of reaching adulthood (ie: final moult). The average life span was 27.5 days, and the maximum recorded was 76 days.

"Relatively older males attracted more females, but once paired they were less likely to mate" (Rodriguez-Munoz et al 2019 p5). So, on any day of observation, older males were more likely to be sharing their burrow with a female than younger males, but the probability of mating was lower based on genetic fingerprinting of the next generation. The problem for females in this annual species, Rodriguez-Munoz et al (2019) concluded, is the lack of a reliable signal of male age. Because of the limited window for mating, females usually mate with any males encountered, and "only a small proportion of individuals ever actually encounter one another..., placing severe constraints on the capacity of females to select long-lived males based on their relative age" (p7).

6.2. SNEAKERS

Where competition for mates is intense, males use alternative reproductive tactics to achieve fertilisation. These involve defending a territory and/or females, or sneaking tactics, as in horned dung beetles (Ota 2019). Males with horns guard the entrances of tunnels containing females, while hornless males construct side tunnels to bypass the guards (Emlen 1997). In this example, evolutionary pressures have maintained two male body types (horned and hornless).

Similarly with many fishes, territorial males have evolved weaponry and sexual display, while sneakers are "commonly small and inconspicuous" (Ota 2019).

Some fishes show substrate-brooding, where females lay their eggs in a male nest and then he externally fertilises them. The territorial males need to be vigilant of sneakers, and sneakers need strategies to get pass the guard before fertilisation (eg: camouflage; moving slowly) (Ota 2019).

Ota (2019) studied a pause-travel (intermittent) locomotion used by sneaker triplefin blenny (Enneapterygius etheostoma) (figure 6.1) that was video-recorded off a beach in Japan. One hundred and sixty sneaking sequences by fifty sneakers from fourteen spawning sites were analysed - of which 117 were detected by the territorial male and 43 were undetected. Territorial males detected sneakers by movement, so pausing was effective as camouflage (small bodies and disruptive patterning of sneakers).

The average pause was 23 seconds, and it began around 270 mm from the spawning site. "Once paused, sneakers need to (re-)start moving, which immediately increases the probability of detection. This may be minimised by moving when the probability of being detected by vigilant animals is low... This idea was supported in the triplefin blenny: sneakers started moving more frequently when territorial males faced away from them than towards them. With a lower probability of detection when starting from behind territorial males, this suggests that sneakers chose such situations to determine when to start moving. In 74% of cases sneakers started moving when territorial males were either in the course of ejaculation, engaged in attacking another sneaker, distracted by other sneakers or facing away from the sneakers" (Ota 2019 p7).

Ota (2019) outlined four phases to the pause-travel sneaking behaviour (which took an average of 80 seconds):

i) Approach spawning site and pause.

ii) Repeated travel-pause locomotion (short movements - average 47 mm).

iii) Rush at female to fertilise as eggs laid, or escape attack of territorial male.

iv) If unsuccessful, begin cycle again, or leave site if successful.

(Source: Izuzuki; https://www.izuzuki.com/)

Figure 6.1 - Triplefin blenny.

6.3. CRAYFISH

The marbled crayfish (figure 6.2) was first detected in 1995, and it holds the unique position of being parthenogenetic (ie: asexually reproducing) among 669 described freshwater crayfish species and 14 756 described decapod crustacean species (Vogt et al 2018).

There is debate over whether to classify it as a pathenogenetic form of slough crayfish (Procambarus fallax), or as a separate species (Procambarus virginalis) (Vogt et al 2018).

Vogt et al (2018) argued for the latter because, although the slough and marbled crayfish are similar in colouration and body proportions, for instance, they differ "considerably with respect to body size, fertility and longevity". There are also minor genetic differences, and the marbled crayfish has invaded all habitats, while the slough crayfish is limited to south-eastern USA. Cross-breeding was not possible between the two species in the laboratory.

(Zfaulkes; in public domain)

Figure 6.2 - Marbled crayfish.

6.4. MISCELLANEOUS

6.4.1. Genitals

Ducks, for example, are predominately monogamous, but, in some species, males employ the strategy of forced extra-pair copulations (FEPCs). "Males looking for FEPC opportunities often form groups that aggregate around fertile females unguarded by their mates. Even if only a single male initiates a sexual chase of a female, other males may join quickly, and the result is a group of males struggling to copulate with the female" (Hegyi et al 2009).

In such species, an "evolutionary arms race" has produced long and highly complex vaginas, and long phalluses (intromittent organ length) (Hegyi et al 2009).

6.4.2. Convergent Evolution

Convergent evolution is where "distinct lineages independently evolve similar traits" (Sackton and Clark 2019 p1). For example, phenotypic convergence in the evolution of echolocation in bats and toothed whales independently as a response to hunting in environments with limited visibility. Namely, at night for bats and deep in the ocean for whales (Sackton and Clark 2019).

"Convergence at the genetic level, of course, can reflect a variety of degrees of similarity, ranging from identical mutations fixed independently in different lineages, to evolutionary changes in the same genes but at different sites, to changes in the same pathways but at different genes" (Sackton and Clark 2019 p1).

6.4.3. Domesticating Foxes

Trut and Dugatkin (2018) described an experiment began in the 1950s by Dimitri Belyaev (with Lyudmila Trut) in Siberia to breed domesticated foxes. In each generation, the calmest individuals were bred, and by the sixth generation "there appeared pups that eagerly sought contact with humans, not only [tail] wagging [but] also whining, whimpering, and licking in a dog-like manner" (Trut et al 2009 quoted in Trut and Dugatkin 2018).

To establish that the changes in behaviour were due to genetics, at the Siberian research institute, Trut took embryos from "tame" mothers and placed them in the womb of "fierce" mothers and vice versa. The pups showed the behaviour of the genetic parents rather than the adopted parents (Trut and Dugatkin 2018).

Subsequently, with the development of DNA sequencing, genes on chromosome 12 of the tame foxes have been found to be similar to those of domestic dogs. "We thus conclude that, through selective breeding over dozens of generations, we have loosely replayed the transformation of a wild canid to a house pet at the genetic level" (Trut and Dugatkin 2018 p33).

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7. WHAT MOTHERS DO

7.1. MATERNAL EFFECTS

"Maternal effects" are aspects of the mother's environment or behaviour that affects the offspring (eg: quality of post-natal care; level of nutrient provisioning for embryo development) (Pruett et al 2019).

Even in species with no maternal care, where the mother lays the eggs and leaves, maternal effects are present in the choice of nest site. In reptile development, for instance, the temperature of the nest site influences the offspring (eg: warmer temperature produces larger offspring) (Pruett et al 2019).

Pruett et al (2019) studied maternal nest site choice of a population of western painted turtles (Chrysemys picta) in Idaho, USA. Daily during the mating season at three sites at Round Lake State Park (near Sagle) from 2013 to 2016, observations and measurements were made (eg: ground temperature where eggs buried). Nest sites were found to be more open (ie: less tree cover) (mean 50% cover) and warmer (mean 25°C) than a random model.

In 2017 the researchers performed an experiment where some eggs were moved to artificial nests in varying open and shaded locations. Egg hatching success increased with openness and temperature.

With both sets of data, there was great variety in hatching success, which suggested to the researchers that intrinsic factors (eg: genes; egg investment) were important as well as the extrinsic factor of nest site choice (Pruett et al 2019).

7.2. BONOBO MOTHERS

The paternity success of a son is increased in bonobos, but not chimpanzees, if the mother is living in the group at the time of the conception of the child (Surbeck et al 2019). "For example, bonobo mothers frequently bring their sons into close spatial proximity with oestrous females, protect their sons' mating attempts from interference by other males, interfere in the mating attempts of other males, and form coalitions with their sons to help them acquire and maintain high dominance rank. Such maternal behaviour is more likely to be effective in bonobos, where the sexes are co-dominant and the highest ranks are consistently occupied by females, than in chimpanzees, where all adult males are dominant over all females" (Surbeck et al 2019 pR354).

Data on four groups of bonobos and seven groups of chimpanzees from various wild and captive studies were analysed by Surbeck et al (2019). Bonobo males with a mother in the group were over three times more likely to sire offspring than males without a mother in the group, whereas there was little difference in the chimpanzee groups.

7.3. SPIDER MILK PROVISIONING

Parental food provisioning is where parents feed the offspring, and this occurs in three forms (Chen et al 2018):

- Direct food sources - Parent(s) capture prey and give to the offspring.
- Regurgitated feeding - Parent(s) eat the prey and regurgitate it for the offspring.
- Specialised food sources - eg: maternal milk (lactation).

Milk is most common in mammals, though the length of provisioning does vary between species. Chen et al (2018) reported a rare case of a jumping spider (Toxeus magnus) that involved milk provisioning.

For the first twenty days of life, the spiderlings do not leave the nest, and the mother releases droplets of a nutritive fluid into the nest ("absolute milk dependence"). Between 20-40 days old, the spiderlings forge during the day, but take milk at night. These observations were based on nineteen nests in the laboratory.

The researchers also manipulated the situation in some of the nests:

i) Blocked milk production, but mother present in nest (maternal care only).

ii) Removed mother from nest (no maternal care).

Blocking milk and removal of mother at birth caused the spiderlings to die.

Removing the mother at 20 days old reduced survivorship of the spiderlings, whereas blocking the milk did not. In the latter case, the spiderlings compensated by foraging themselves more. So, overall, "milk provisioning after 20 days does not affect adult survivorship, body size, sex ratio, and development time, but the mother's presence plays a key role in assuring high adult survival and normal body size" (Chen et al 2018 p1054).

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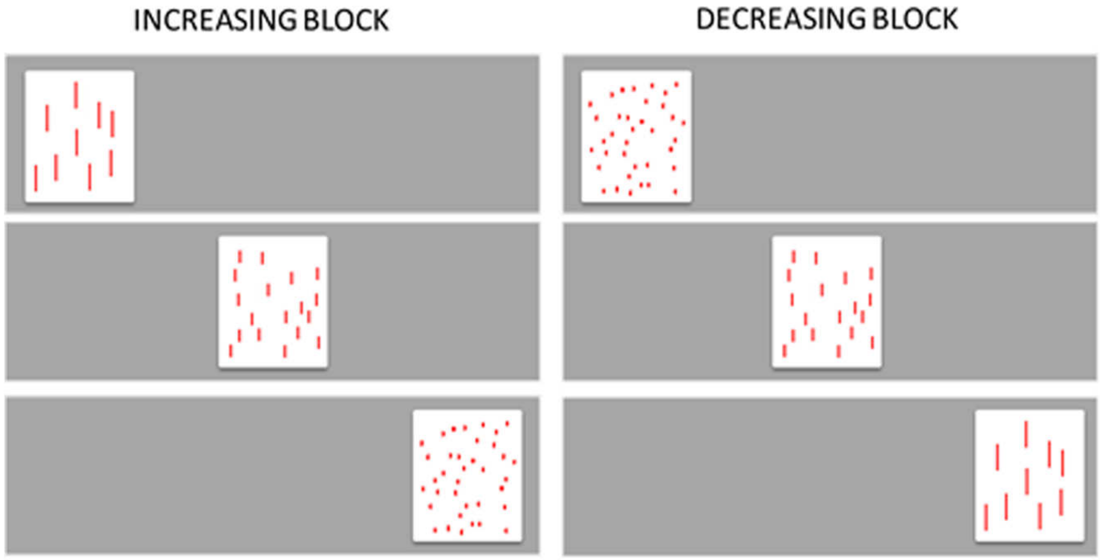
8. MENTAL NUMBER LINE

The "mental number line" (MNL) (Dehaene 2011) is the idea that humans represent smaller values on the left and larger ones on the right (Rugani et al 2015).

Seven month-old infants, for example, prefer increasing numbers displayed left to right over decreasing values from left to right (de Hevia et al 2014) (figure 8.1), "showing that spatial-numerical association does exist before mathematics and linguistic education" (Rugani et al 2015 p534) [12].



(Source: de Hevia et al 2014 figure 4)

Figure 8.1 - Stimuli presented to human infants.

In terms of non-human animals, the tendency to count from left to right has been found in chicks. Rugani et al (2015) trained three day-old domestic chicks (Gallus gallus) to reach a food reward associated with a target number (eg: "5" - 5 spots). Then the chicks were presented with a left and right panel to choose from. The

[12] "Brains" evolved to gather, store, and respond to information, probably as organisms actively explored their environments, and with the selective pressure of predation (Sole et al 2019). The "solid brain" is a cognitive network with "static sets of neurons linked in an adaptive web of connections. These are 'solid' networks, with a well-defined and physically persistent architecture" (Sole et al 2019 p1).

There is an alternative to this, Sole et al (2019) noted: "Other systems are formed by sets of agents that exchange, store and process information but without persistent connections or move relative to each other in physical space. We refer to these networks that lack stable connections and static elements as 'liquid' brains, a category that includes ant and termite colonies, immune systems and some microbiomes and slime moulds" (p1).

panels were presented as a smaller number than the target (eg: "2") or a larger number (eg: "8"). In the former case, pecking the left panel supports the MNL (chosen 70% of the time by the chicks), and the right panel in the latter case (chosen 70% of the time). "The association of a certain number on the left or on the right was not absolute but depended on the relative magnitude of the number with respect to the target. Chicks that had experienced the number '5' as the target, associated the number '8' with the right side of space. On the contrary, chicks that had experienced the number '20' as the target, associated the number '8' with the left side of the space" (Rugani et al 2015 p535).

Rugani et al (2015) summed up: "Our results indicate that a disposition to map numerical magnitudes onto a left-to-right–oriented MNL exists independently of cultural factors and can be observed in animals with very little non-symbolic numerical experience, supporting a nativistic foundation of such orientation. Spatial mapping of numbers from left to right may be a universal cognitive strategy available soon after birth. Experience and, in humans, culture and education (eg: reading habits and formal mathematics education) may modulate or even be modulated by this innate number sense" (p536).

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9. PET OWNERSHIP

9.1. INTRODUCTION

Pet ownership demographics are collated by the "pet industry" as well as by academic researchers. Table 9.1 gives examples from the USA (Simring 2018).

PET	CHARACTERISTICS
Dog	Extravert (compared to cat owners) Less educated (compared to non-dog owners)
Cat	Neurotic (compared to dog owners) Higher educated (compared to non-cat owners)
Bird	Socially outgoing, socially dominant if female (compared to horse, turtle, and snake owners)
Horse	Higher educated (compared to other pet owners) Assertive (compared to turtle, snake, and bird owners)
Cold-blooded exotic pets	Unconventional, if female, and hardworking, if male (compared to horse, turtle, and bird owners)
Any pet	Families (with or without children) Sociable
Non-pet owners	Self-reported as independent Higher educated

Table 9.1 - Examples of demographics linked to pets in the USA.

9.2. NATURE OR NURTURE

There is evidence that animal companionship is innate, including:

a) LoBue et al (2013) - Toddlers given a choice of toys or live animals spent more time interacting with the latter (appendix 9A).

b) Stoeckel et al (2014) - Similar areas of the brain are active when women view images of their own child, and their pet dog (appendix 9B).

c) Nittono et al (2012) - Viewing images of baby animals increased focus attention. Students performed a task that required attention before viewing images of adult or baby animals, or food, and then repeated the task. Task performance improved only after viewing the baby animals (appendix 9C).

Wilson (1984) referred to the idea of "biophilia" - "an inherent tendency to focus on life and life-like processes" (Yuhas 2018). Pets link to the innate motivation to care for fragile, young infants, for instance (Yuhas 2018).

There are also cultural influences on pet ownership, including:

a) Different views around the world - eg: dogs considered unclean in some cultures (Yuhas 2018).

b) Choice of dog breeds in the USA, for example, linked to those seen in movies of the time rather than a breed's health, longevity or behaviour traits (eg: trainability) (Herzog 2014).

9.3. TWO BENEFITS OF PET OWNERSHIP

i) Psychological support.

Eg: Cat and dog owners less stressed when pet present during challenging word test (Zilcha-Mano et al 2012). But this did depend on the perceived closeness of the relationship with the animal (Yuhas 2018).

ii) Therapy.

Building on the general benefits of pet ownership is animal-assisted therapy (AAT) (defined as "the use of an animal as either a treatment by itself or an addition to an existing treatment, such as psychotherapy" (Lilienfeld and Arkowitz 2018 pp24-25). Popularised in the 1960s by Boris Levinson, it has been calculated that around one-fifth of US therapists incorporated animals into their treatment in some way (Lilienfeld and Arkowitz 2018).

Many claims are made for the benefits of AAT, but Lilienfeld and Arkowitz (2018) asked it works. This would require evidence of changes to psychological health beyond the short-term pleasure, relaxation, and excitement of interacting with "friendly animals" (Lilienfeld and Arkowitz 2018).

Dolphin-assisted therapy (DAT) is well researched. It is often used with children with autism and/or learning disabilities. Marino and Lilienfeld (2007) reviewed the evidence, and found little to support its effectiveness. Part of the problem was methodological weaknesses in the studies, like being short-term only or lacking comparison groups with other animals or objects. Lilienfeld and Arkowitz (2018) noted the costs of DAT - financially, to the child (eg: infectious disease from the animals), and to the dolphins (eg: taken from the wild).

9.4. DOGS

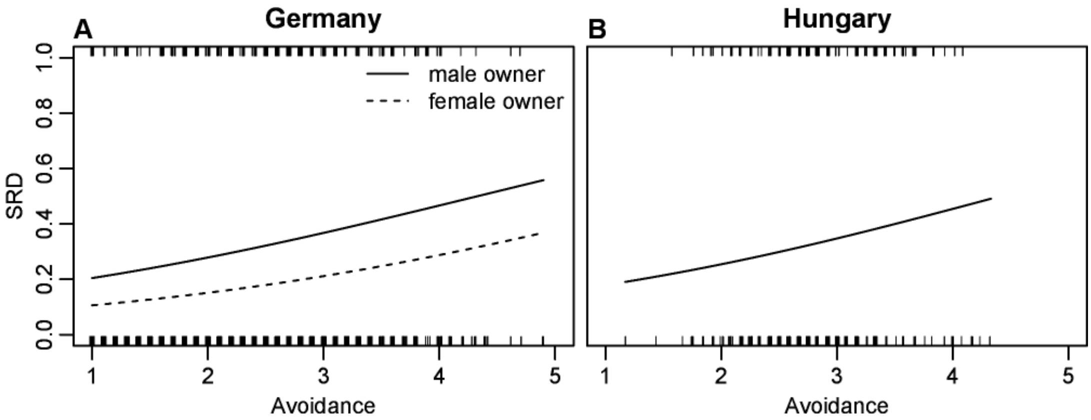
The success of dogs as pets includes their ability to form attachments to their owners, similar to the human parent-child attachment (Miklosi 2018).

Topal et al (1998) found that dogs in the "strange situation test" showed similar behaviours to infants. This test is a measure of the attachment between the parent, usually the mother, and the child. For example, an infant alone is afraid of a friendly stranger, but not if the parent is present (appendix 9D).

If dogs can form attachments to humans as in human child-parent attachments, then separation-related disorder (SRD) can occur as in human separation anxiety. "This phenomenon occurs in the owner's absence or when the dog is prevented access to the owner. Owners of dogs with SRD complain most frequently about destructive behaviour displayed at home, excessive vocalisation (often noticed by neighbours), or inappropriate elimination (urination/defecation). Further symptoms (which are less easily recognised) include autonomic signs such as hypersalivation or hyperventilation, increased and repetitive motor activity (eg: pacing, circling), repetitive behaviour (eg: over-grooming or self-mutilation), behavioural signs of depression such as withdrawal, inactivity or inappetence [loss of appetite], gastrointestinal symptoms (vomiting, diarrhea) or escape behaviour that can result in self-trauma" (Konok et al 2015 p2).

The human caregiver's behaviour can influence the development of separation anxiety in children, so the dog owner's behaviour can play a role in SRD. Konok et al (2015) focused on the owner's attachment style and neuroticism with questionnaires completed by 323 Hungarian and 1185 German dog owners. The questionnaire included items about the dog's behaviour as well as their own (eg: fear of abandonment).

Around a quarter of the dogs were classed as having SRD, and their owners were significantly more likely to have an insecure-avoidance attachment (eg: less responsive to dog's needs) (figure 9.1). "None of the human personality scales influenced SRD in dogs significantly in either dataset" (Konok et al 2015 p8).



(Source: Konok et al 2015 figure 1)

Figure 9.1 - The likelihood of the dog showing SRD based on the level of insecure-avoidance attachment of the owner.

Konok et al (2015) summed up: "We suppose that owners' attachment style influences their care-giving behaviour toward the dog: they may show a less consistent responsiveness to the dog's needs. Owners with insecure-avoidant attachment style avoid intimate contacts, closeness and affection and it is possible that they behave in this way not only in their interpersonal relationships but also toward their dogs. Dogs who meet refusal or ignorance of their needs (eg: need for contact) can learn that they cannot be sure about the availability of the owner" (p8).

It also helps that dogs show clear emotions, though the attribution of owners plays an important part. Horowitz (2009) tested the anthropomorphism of owners attributing a "guilty look" as the dog feeling guilty after doing a forbidden behaviour. Anthropomorphism occurs when "animal behaviour is compared to human behaviour, and where there is superficial matching, the attribution (of understanding, emotion, or knowledge) that is made to the human is extended to the animal" (Horowitz 2009 p447).

Horowitz (2009) continued: "In other words, the anthropomorphism includes the suggestion that dogs not only look guiltily, but that this indicates that dogs feel guilty or realise their misdeed if they have done something wrong, inappropriate, warned against, or otherwise violative of an established code of behaviour. Owners take behavioural evidence, or the outward appearance of the animal, to be conveying information about the animal's understanding or experience" (p448).

For the experiment, Horowitz (2009) recruited fourteen dog owners in New York by publicly displayed flyers, in local dog parks, and online. Only single-dog households, and trained dogs were involved. Presented as a test of "obedience at a distance", the dog was presented with a biscuit which the owner told them not to eat before leaving the room for twenty seconds. When the owner returned, the experimenter tells them if the dog had obeyed. While the owner was out of the room, the experimenter either gave the dog the biscuit or removed it, which meant that there were two true and two false information conditions:

- 1 - Dog eats treat/owner told obeyed and did not eat (false information to owner).
- 2 - Dog eats treat/owner told disobeyed and ate (true).
- 3 - Dog does not eat treat/owner told obeyed (true).
- 4 - Dog does not eat treat/owner told disobeyed (false).

Horowitz (2009) was interested in whether the owners would attribute a "guilty look" to the dog. Nine behaviours were associated by owners with the "guilty look" (eg: avoiding eye contact; moving away from the owner). The rating of these behaviours did not vary whether the dog was actually guilty or not (ie: disobeyed or obeyed commend to not eat the biscuit). These behaviours, "though identified as expressions of guilt by owners, were more often associated not with guilt on the dog's part, but with the perception of guilt on the owner's part" (Horowitz 2009 p450). Owners reported an average of 2.4 "guilty look" behaviours when they believed the dog had disobeyed compared to 0.6 when obeyed.

More "guilty look" behaviours were seen when the dog was scolded for disobeying, suggesting that the scolding behaviour cause these behaviours.

Horowitz (2009) ended: "It is worth noting that the present results do not indicate that domestic dogs do not experience guilt. All that behavioural research can investigate is the rate and context of specified actions: in this case, the rate of the behaviours variously implicated in the guilty look. What is indicated is that what humans interpret as an expression of guilt or an understanding of disobedience is the result of a (learned or instinctive) response to the appearance of a cross or scolding human" (p451).

Along with similar studies (eg: Hecht et al 2012), "findings to date suggest that dogs engage in guilt-seeming behaviour when they sense that something will elicit an owner's displeasure and hope to avoid a breach in the relationship" (Hecht 2018 p43).

Further to the dog's social competence, which aids the human-pet relationship, are learning, and co-operation with humans and with other dogs (Miklosi 2018). The dog's sociability towards humans has been linked to a oxytocin gene (Kis et al 2014). Oxytocin is released in social interactions, and in human creates feelings of connectedness (Hecht 2018) [13].

9.5. APPENDIX 9A - LOBUE ET AL (2013)

Experiment 1 - To investigate "children's natural affinity for animals" with 38 11-40 month-olds. The children were individually placed in a room containing fourteen small toys and two live animals (a hamster in a cage and a fish in a fishbowl) for 5-10 minutes. The behaviour of the child was observed and scored (eg: time spent playing with an item).

The children had more frequent interactions with the animals than the toys (in total, over 100 for each of the animals and less than 100 each of for the toys).

But this study was exploratory, and limited in its experimental controls (eg: fourteen toys vs two animals).

Experiment 2 - This experiment was more rigorous with four toys and four animals for the 38 18-36 month-olds to interact with. The animals were a hamster and a fish (non-threatening), and a tarantula and a snake in their own enclosures (threatening). The children spent five minutes playing alone, and five minutes playing with a parent.

Both the child alone and the parent and child together interacted more often with the animals than the toys (mean 16.8 vs 8.3 interactions per person). There was more interaction with the non-threatening than threatening animals.

Experiment 3 - This experiment added another level of rigor by offering the children the same toy or live animal to look at - caged hamster/stuffed hamster, fish in bowl/plastic fish, or caged green gecko/plastic gecko. The participants were twenty 18-33 month-olds.

The children spent more time focusing on the live than toy animal (mean 38.7 vs 14.2 seconds). "The results demonstrate that children spend more time interacting with animals than with toys even when they cannot directly manipulate them" (LoBue et al 2013 p66).

The researchers noted one point about methodology - "we did not control for animacy. We could have used

[13] A dog has 430 million neurons in the cerebral cortex and a cat 250 million (compared to 16 billion in humans) (Fischman 2018), does that mean dogs are smarter than cats?

comparison stimuli that were also animate, such as robotic or otherwise moving toys to control for animacy... However, even though this would have provided a more stringent control, motion produced by artefacts is quite different than the movement produced by living things" (LoBue et al 2013 p68).

9.6. APPENDIX 9B - STOECKEL ET AL (2014)

Aim - To analyse patterns of brain activity when mothers view images of their own child and of their own dog.

Method - Fourteen female volunteers (aged 22-45 years old) in the Massachusetts area where recruited, who had a child aged 2-10 years old and a pet dog for at least two years.

The participants were placed inside a functional magnetic resonance imaging (fMRI) scanner, and shown pictures of their own child, their own dog, an unfamiliar child, and an unfamiliar dog. The fMRI scanner measures blood oxygen levels in different areas of the brain, and these are taken as signs of brain activity.

Findings - Viewing their own child and dog (compared to the unfamiliar images) showed similar activity in areas of the brain related to emotions, reward, and affiliation (figure 9.2). But there were differences when viewing own child and own dog (eg: fusiform gyrus more active when viewing own dog than own child).

Conclusion - "These results demonstrate that the mother-child and mother-dog bond share aspects of emotional experience and patterns of brain function, but there are also brain-behaviour differences that may reflect the distinct evolutionary underpinning of these relationships" (Stoeckel et al 2014 p11).

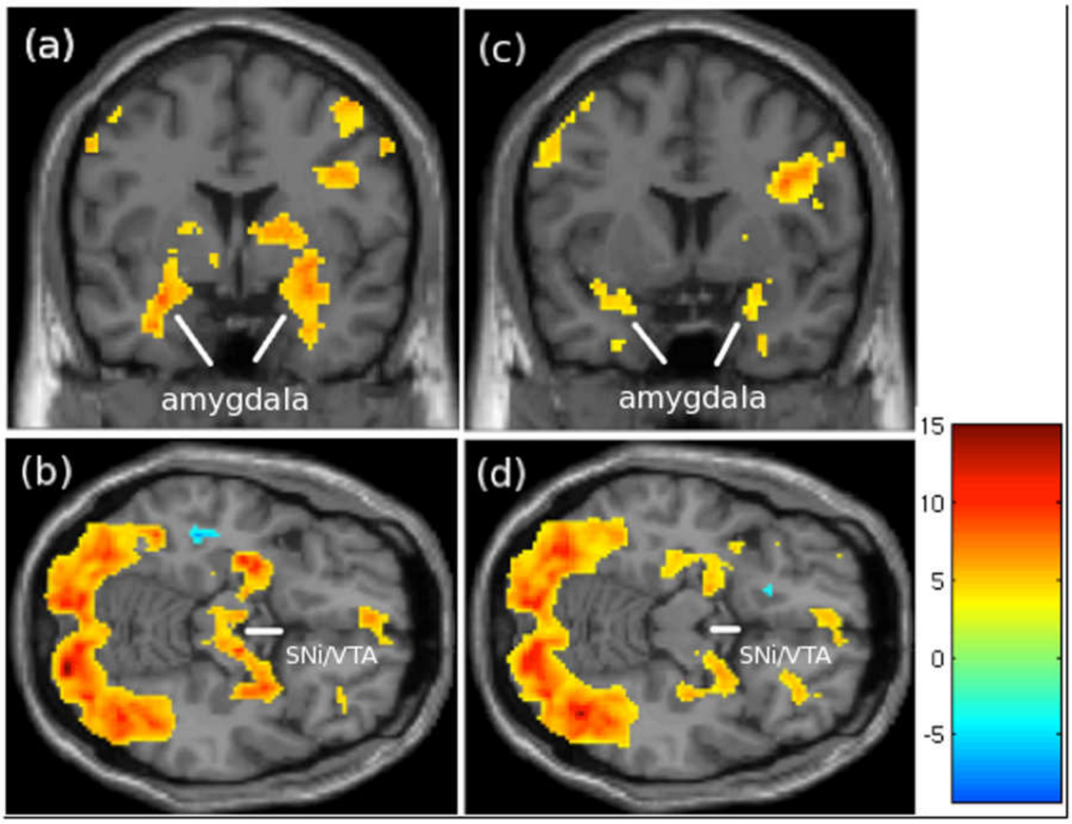
Evaluation

(+)

- Within-participant design.

- Controlled protocol ("which isolated the faces of dogs and children without including other features or contexts in the image that could complicate the interpretation of results if participants selected their own images from an existing set of photographs..."; Stoeckel et al 2014 p11).

- Standardised equipment and procedure.



(SNi/VTA = substantia nigra/ventral tegmented area)

(Source: Stoeckel et al 2014 figure 3)

Figure 9.2 - Brain activation in response to images of own child (a and b) and own dog (c and d).

(-)

- Cross-sectional study (difficult to establish causation).

- No measurement of attachment between mother and child.

- Homogeneous sample of volunteers.

- Generalisability of findings to fathers or adopted parents, or other animal species not possible.

- Uncontrolled variables (eg: menstrual phase; Stoeckel et al 2014).

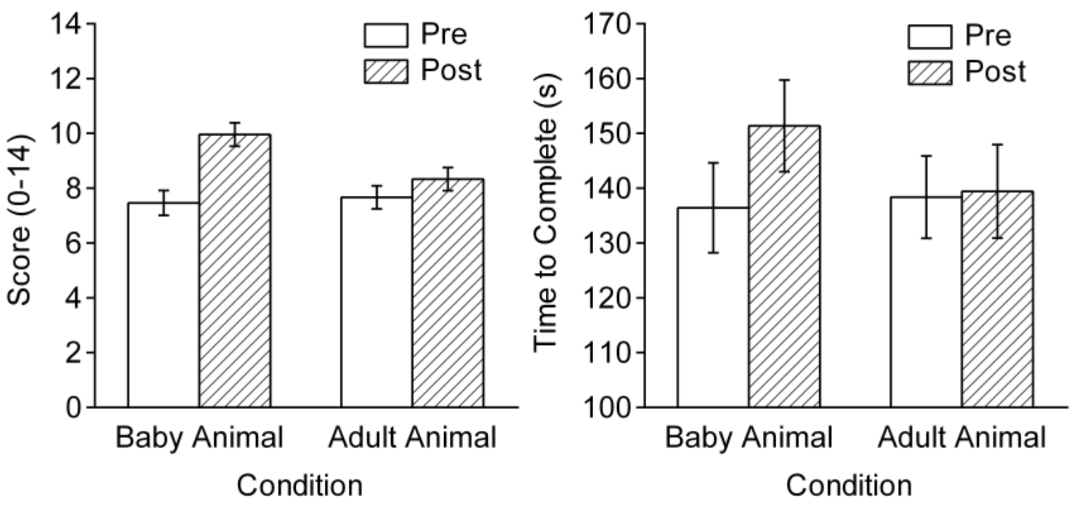
9.7. APPENDIX 9C - NITTONO ET AL (2012)

Cute (or kawaii in Japanese; Nittono et al 2012) is associated with babies. "This is a set of features that are commonly seen in young animals: a large head relative to the body size, a high and protruding forehead, large eyes, and so forth. Lorenz [1943] assumed that responses to baby schema are innate processes and are triggered by elemental features of the stimuli. In humans, the stimuli are deemed cute, capture attention, bring a smile to the viewer's face, and induce motivation and behaviour for approach and caregiving" (Nittono et al 2012 p1).

Nittono et al (2012) performed three experiments on viewing cute images and subsequent unrelated behaviour.

Experiment 1 - Forty-eight Japanese university students were randomly allocated to "baby animal condition" or "adult animal condition". All participants played a children's game which involved removing with small tweezers fourteen plastic pieces from holes without hitting the edges of the holes or dropping the piece. This task was performed before and after viewing images - seven pictures of puppies and kittens (baby animal condition) or adult dogs and cats.

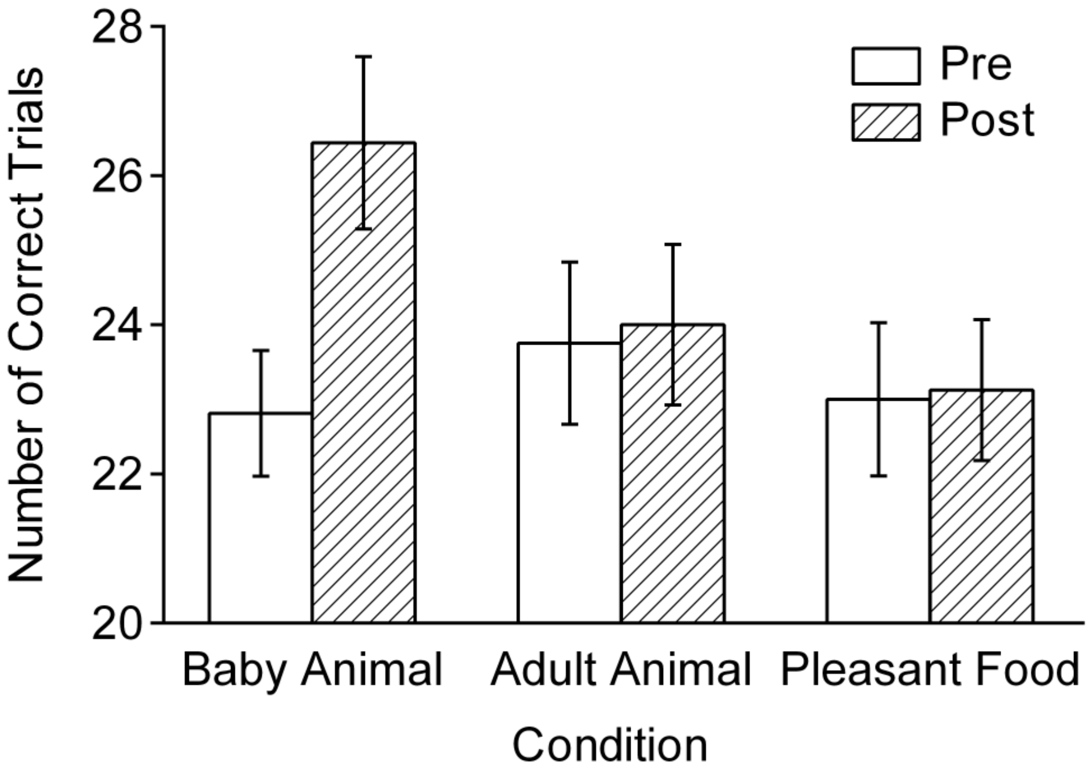
All participants improved their performance between the first and second tasks (ie: less errors), but this was significantly different for the baby animal condition, and these participants took longer post-images (figure 9.3). "This finding suggests that viewing cute images makes participants behave more deliberately and perform tasks with greater time and care" (Nittono et al 2012 p3).



(Source: Nittono et al 2012 figure 1)

Figure 9.3 - Mean scores (ie: correct pieces retrieved) and time to complete the task before and after viewing the images in Experiment 1.

Experiment 2 - Forty-eight more students searched for a target digit in a matrix of numbers in a certain time period. Inbetween the two performances of the task, participants viewed pictures of baby animals, adults animals (as in Experiment 1), or pleasant foods. Performance significantly improved in the baby animal condition (figure 9.4).



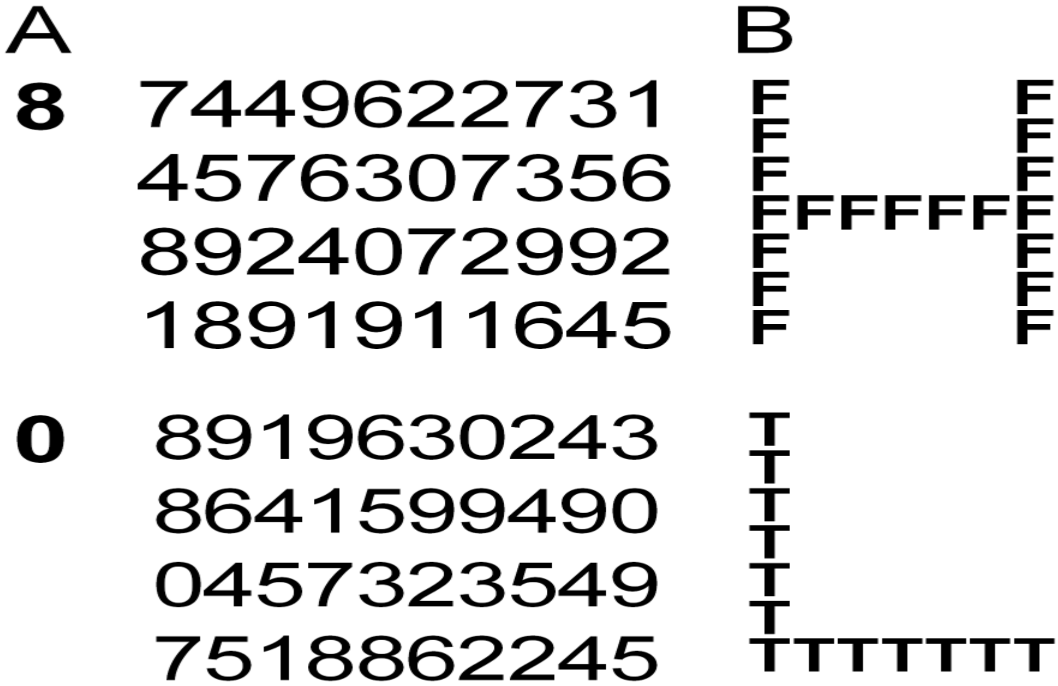
(Source: Nittono et al 2012 figure 3)

Figure 9.4 - Mean number of correct visual searches before and after viewing images in Experiment 2.

Experiment 3 - Another 36 students performed a reaction time task after viewing images of baby animals, adult animals, or neutral objects. The reaction time task was to say as quickly as possible what a large or small letter was (figure 9.5).

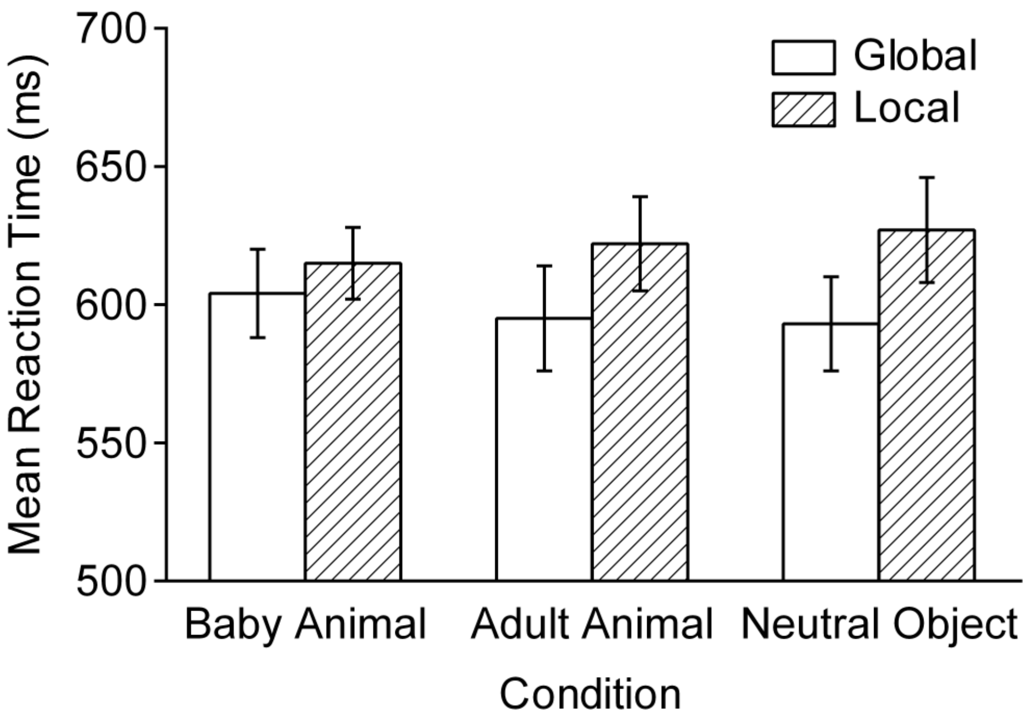
Participants in the baby animal condition were significantly faster than the other two groups at recognising the small (local) letters, but slower on the larger (global) ones (figure 9.6). This fits with the idea that participants in this condition narrowed their attention.

Sherman et al (2009), whose work Nittono et al (2012) replicated, explained the findings of all the experiments with the "embodied cognition perspective", "which holds that the tenderness elicited by cute images is more than just a positive affective feeling state, but it can make people more physically tender in their motor behaviour" (Nittono et al 2012 p6).



(Source: Nittono et al 2012 figure 2)

Figure 9.5 - Stimulus material in (a) Experiment 2 and (b) Experiment 3.



(Source: Nittono et al 2012 figure 4)

Figure 9.6 - Mean reaction times in Experiment 3.

However, Nittono et al (2012) went further: "This study does not deny the view that cuteness is related to embodied cognition and sociality motivation. Rather, this study provides further evidence that perceiving cuteness exerts immediate effects on cognition and behaviour in a wider context than that related to caregiving or social interaction" (p60).

There are three wider methodological issues outlined by Nittono et al (2012):

i) The psychophysiological state underlying the feeling of cuteness. Nittono et al (2012) did not take physiological measures, but other research has found increased heart rate and respiratory rate ("implying increased arousal"; Nittono et al 2012) when viewing baby animals (eg: Shiota et al 2011).

ii) Gender differences - Though female participants in these experiments gave higher cuteness ratings to the images, there were no mean differences between men and women in performance of the tasks. The difference in cuteness ratings "may not be directly linked to an overt behaviour or may not be strong enough to produce behavioural differences. The sensitivity to cuteness cues also varies among women depending on their hormonal states" (Nittono et al 2012 p7).

iii) Cultural differences - Nittono et al (2012) observed that "it has been suggested that the attitudes and responsiveness toward infants and babies differ between cultures. Japan's culture accepts and appreciates childishness at the social level" (p7).

9.8. APPENDIX 9D - TOPAL ET AL (1998)

The "Strange Situation Test" (SST) was originally designed by Ainsworth and Wittig (1969), and it distinguished three types of infant-parent attachment:

- Secure - child misses parent upon separation, greets parent on reunion and then settles. Fear of stranger when alone, but not when with parent.

- Insecure-avoidant - no distress at separation and ignores parent on reunion.

- Insecure-resistant - highly distressed by separation which continues even at reunion.

Topal et al (1998) used 51 dog owners in Hungary who volunteered for the research. The SST involved seven episodes (each lasting two minutes):

* 1 - Owner and dog settle in experimental room.
* 2 - Stranger enters and interacts with owner and the dog, before leaving again.
* 3 - Owner leaves, and stranger enters and interacts with the dog.
* 4 - Owner returns and stranger leaves.
* 5 - Dog alone.
* 6 - Stranger enters and interacts with dog.
* 7 - Owner returns and stranger leaves.

Two trained observers scored the dogs' behaviours on eight categories (eg: playing; passive behaviours). The behaviours were then grouped into three:

i) "Degree of anxiety" - "Individuals that scored high on this factor behaved passively (ie: they did not play and spent long amounts of time exhibiting passive behaviours in the presence of the stranger compared with the owner) and strove for physical contact with the owner" (Topal et al 1998 p223).

ii) "Acceptance of the presence of the stranger" - Contact seeking with the stranger.

iii) "Attachment" - Contact seeking with the owner.

These groups were seen as parallels to the human attachment types, and table 9.2 outlines the main characteristics.

	Anxiety	Acceptance	Attachment
Playing when owner present	Very low	Low	Yes
Playing when stranger present	Very low	Yes	Low
Passive behaviour when owner present	High	Low	Little
Passive behaviour when stranger present	High	Some	Little
Physical contact with owner	High, but delayed on reunion	Yes, small delay	Yes, immediate
Physical contact with stranger	Some	High	Low

(Based on Topal et al 1998 table 2 p224)

Table 9.2 - Main characteristics of the three types of attachment behaviour by the dogs.

Rehn et al (2014) reported a correlation between the human-completed Monash Dog Owner Relationship Scale (MDORS), which measures the perceived closeness of the dog-owner relationships, and level of physical contact on reunion in the SST. But from the dog's point of view, this could be a strong attachment or a reflection of past rewards of physical contact (Goldman 2018) [14].

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[14] Howard (2019) divided love into different types (as described by the Ancient Greeks) in her attempt to answer if pets love their owners. For example, "storge" (love between family members) is seen in the attachment behaviour of dogs and the presence of oxytocin. The other forms of love include "eros" (erotic love), "philia" (friendship loyalty), and "philautia" (love for the self) (Howard 2019).

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