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ANIMAL BEHAVIOUR: ADVANTAGES AND DISADVANTAGES NO.5

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CONTENTS

1. PARTHENOGENESIS

1.1. INTRODUCTION

The dominant mode of reproduction for multi-cellular animals is sexual reproduction, except for the approximately 1% of species that produce offspring from unfertilised eggs (known as parthenogenesis) (Nakano et al 2019).

Obligate parthenogenesis (or asexual reproduction) is where offspring develop from unfertilised eggs, and facultative parthenogenesis (FP) is the ability to reproduce asexually or sexually [1]. Obligate sexual reproduction is when mating is the only strategy (Burke et al 2015).

Generally, pathenogenesis was believed to be rare (eg: females alone in captivity), but more cases are being found in the wild (eg: boa constrictors, pit vipers, turkeys (table 1.1) [2]), even when plenty of males are available (Pilcher 2013).

- Parthenogenetic development in turkey eggs is initiated in 1 to 30% of unfertilised eggs, "although development is completed only in a small percentage of parthenogens... In most cases, the embryo, which dies within 24 h of incubation, is an unorganised sheet of epithelial cells [3] " (Cassar et al 1998 p1463). This is similar to "positive development", where fertilised eggs "exhibit rudimentary development and often die within the first 24 to 48 h of incubation. Typically, the development in these embryos is unorganised and the embryonic tissue is a sheet of epithelial cells overlying the yolk" (Cassar et al 1998 p1463). Some researchers have viewed these two processes as "alternative classifications of the same phenomenon" (Cassar et al 1998 p1464).

Table 1.1 - Turkeys and parthenogenesis.

Parthenogenesis allows a species to grow faster as animals can spend more time looking for food rather than mates, and the dangers of mating are removed (eg: disease

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[1] There is also cyclical parthenogenesis (eg: seasonal alternations between sexual and asexual reproduction) (Stelzer and Lehtonen 2016).

[2] However, Sites et al (2011) stated that true parthenogenesis among vertebrates is known only in some squamata (lizards and snakes).

[3] Outer layer of a body in development.

or injury by male). A new combination of genes from sexual reproduction may not be any better than the current set (Pilcher 2013).

On the downside, all-female species produced by parthenogenesis are likely to go extinct after 10 000 - 100 000 generations (Pilcher 2013). No sexual reproduction means no shuffling of genes, and harmful mutations have an effect on survival of the species [4]. The offspring of parthenogenesis are severely inbred, and their survival is limited. For example, a captive female zebra shark in the Burj Al Arab aquarium in Dubai produced over a hundred eggs over several years with only four surviving (Pilcher 2013) (table 1.2).

ADVANTAGES	DISADVANTAGES
1. No need to find mate and risks involved, including injury and coercion from aggressive males. 2. Can grow faster by concentrating on finding food. 3. A strategy for isolated females or lack of males. A combination of genes as in sexual reproduction may be no better than clones.	1. No shuffling of genes, so the risk of harmful mutations persisting over generations, and even extinct. 2. Very inbred offspring with risk of recessive gene conditions. 3. Still a risk of aggressive males and coercion until a species is completely parthenogenetic.

Table 1.2 - Main advantages and disadvantages of parthenogenesis.

1.2. STICK INSECTS AND FACULTATIVE PARTHENOGENESIS

Two main theories for the asexual reproduction aspect FP have been proposed (Burke et al 2015):

a) Mating scarcity hypothesis - Mating opportunities are rare or impossible [5]. This "assumes that sex is the selectively favoured or 'preferred' mode of reproduction, and that females that engage in parthenogenetic reproduction merely make the best of a bad (ie: mateless) situation" (Burke et al 2015 p117).

b) Sexual conflict hypothesis - The cost of mating to the female is high (eg: injury), and females evolve

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[4] Because the offspring are clones of the mother, they will carry the same detrimental mutations, and, as in asexual populations generally, this will produce lower evolutionary fitness. This has been called the "mutational ratchet" (Muller 1964) or "mutational melt-down" (Lynch and Gabriel 1990).

[5] For example, lack of mating opportunities triggers parthenogenesis in Komodo dragons (Watt et al 2006).

strategies to resist males.

The New Zealand-based smooth stick insect (Clitarchus hookeri) is an example of FP. Sexual populations occur on the North Island (ie: facultative parthenogenesis), and "pure" parthenogenetic populations on the South Island, mostly (Nakano et al 2019).

The sexual populations show a "scramble competition" mating system. Females signal their availability, and males race to mate with as many females as possible. After copulation, males "mate guard" by clinging to the females for a few hours and then leave. Males with strong movement ability (eg: small body with long legs) and specialised senses (eg: long antennae to detect females' chemical signals) have an advantage (Nakano et al 2019).

In laboratory experiments, Nakano et al (2019) found that the "pure" parthenogenetic females still maintained behaviours related to sexual reproduction (eg: chemical signalling), and males were unable to distinguish between the females with a given a choice of two (ie: "a preference for smaller females regardless of their reproductive mode"; Nakano et al 2019 p13).

Burke et al (2015) tested another FP species of stick insect - the Australian spiny leaf stick insect (Extatosoma tiaratum). In their experiment, virgin females were kept in one of three conditions - with a male (sexual reproduction condition), with another female (parthenogenesis condition), or initially with a female who was later switched for a male (interrupted condition).

Females paired with males showed strong resistance behaviour to mating (eg: curling abdomens tightly over backs; kicking male to dislodge). Females in the interrupted condition had reduced egg output and higher mortality than the other two conditions. But "eggs of interrupted females showed a trend towards higher early hatching success, and the offspring of interrupted females were more likely to survive to the second instar than offspring of parthenogenetic females, suggesting that indirect benefits might compensate to some extent for the direct costs of reproductive switching. None the less, parthenogenetic females stopped signalling their reproductive status to males, and females forced to switch from parthenogenesis to sex exhibited exaggerated and sustained defensive behaviour (abdomen curling) in the presence of males. These results suggest that parthenogenetic females are selected to avoid males and, if they encounter males, to minimise mating rate" (Burke et al 2015 pp123-124). Females also produced a repugnatorial secretion to repel the males.

The results supported the sexual conflict hypothesis for FP. Burke et al (2015) stated: "It is also possible that facultative parthenogenesis is rare because males tend to 'win' sexual conflicts more frequently than females, by achieving matings despite female resistance... A parthenogenetic strategy might only persist if it actually allows females to avoid the costs of sex. If harassment by males cannot be avoided, then females might gain very little from parthenogenesis and might actually incur greater costs if resistance results in increased harassment, or if it fails to prevent matings. Thus, sexually antagonistic co-evolution might help to explain why obligate sex is so widespread compared to parthenogenesis" (Burke et al 2015 p125).

1.3. HYMENOPTERA

Hymenoptera is an order of insects that includes bees, wasps, and ants [6], and "social and solitary alike, parthenogenesis is part of the regular life cycle, in which males develop from unfertilised eggs, ie: via arrhenotokous parthenogenesis, and females develop from fertilised eggs. Arrhenotoky and haplodiploidy (males are haploid and inherit a single set of chromosomes from their mother, whereas females are diploid and inherit one set of chromosomes from each parent) usually coincide in Hymenoptera and are often regarded as synonymous" (Rabeling and Kronauer 2013 p274). Thelytokous parthenogenesis, where females develop from unfertilised eggs, does occur but more rarely (Rabeling and Kronauer 2013).

In some species, queens can produce daughters parthenogenetically, but workers sexually. This has the advantage of "maintaining the genetic variation within the worker force, ie: those members of the colony that mostly interact with the external environment" (Rabeling and Kronauer 2013 p274).

Parthenogenesis produces offspring that is identical to the mother. But over time mutations occur leading to genetic divergence (known as the "Meselson effect"; Welch and Meselson 2000) (Rabeling and Kronauer 2013).

There is another variation called "male clonality", where queens produce males sexually that are genetically identical to her mate (but it is not entirely clear how this happens) (Rabeling and Kronauer 2013). "As a consequence, males and queens maintain entirely separate gene pools that combine only to produce workers. These systems are suggested to represent the end point of a molecular arms race between males and females, which

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[6] In taxonomic terms, an individual species will be part of a genus, which will be part of a family, and in term part of an order.

would make them unique model systems for the study of sexual conflict" (Rabeling and Kronauer 2013 p275).

With separate gene pools, it allows queens to mate with their brothers without the problems of inbreeding. It is useful in small colonies or founding populations (Rabeling and Kronauer 2013).

The variations in sexual reproduction in Hymenoptera include (Rabeling and Kronauer 2013) [7]:

- Females (queens or workers) produce males by arrhenotokous pathenogenesis.
- Male clonality.
- Queens produce queens by thelytokous parthenogenesis.
- Queens produce workers by sexual reproduction.
- Queens produce workers by thelytokous parthenogenesis.
- Workers produce queens by thelytokous parthenogenesis.
- Workers produce workers by thelytokous parthenogenesis.

Rabeling and Kronauer (2013) noted the association between thelytokous parthenogenesis and social parasitism, as in the Cape honeybee. Workers invade the colonies of another African honeybee sub-species and immediate start laying eggs. The hosts do not detect these eggs, which are raised to adulthood, and "the newly emerged workers produce more parasitic daughters, causing the decline and ultimately the collapse of the host colony" (Rabeling and Kronauer 2013 p286).

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[7] Around 125 000 species are known, and there are estimates of 5-10 times more to be discovered (Rabeling and Kronauer 2013).

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2. FEIGNING DEATH

2.1. OVERVIEW

Acting dead (tonic immobility (TI), death feigning, thanatosis, "playing possum" or "animal hypnosis" [8]) is used by animals for various reasons.

1. As an anti-predator strategy - eg: Hognose snake secretes a foul-smelling fluid and even blood, while Virginia opossum lies in a prone posture with drooling, and a tongue-lolling grimace (Edmonds 2019). "Many predators will not take carrion or are not stimulated by immobile prey" (Barnard 1983).

2. In sexual situations - The female moorland hawker dragonfly (Aeshna juncea) feigns death after mating with one male to avoid further sex with other males (Edmonds 2019). Certain butterflies show TI by females to avoid coercion (Humphreys and Ruxton 2018).

In another situation, Hansen et al (2008) observed TI by male nursery web spiders sometimes during copulation. The male provides food for the female ("nuptial gift"), who consumes it, and the male transfers sperm meanwhile. If the female stops eating, some males entered a state of TI until the female returned to eating. Sexual cannibalism is rate in this species, so it is not clear why the males show TI (Humphreys and Ruxton 2018).

TI by males has been noted in some species with female post-copulation cannibalism (Humphreys and Ruxton 2018).

3. To capture prey - eg: certain species of cichlid lie at the bottom of the river to prey upon fish that come to scavenge their body (Edmonds 2019).

Humphreys and Ruxton (2018) reported the use of TI by adult fish to catch prey in two species of cichlid,

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[8] Animal hypnosis was first described in the 17th century (Sargeant and Eberhardt 1975).

and the comb grouper fish.

4. Other - TI has been reported in social insects to avoid aggression. For example, in a stingless bee, surplus queens risk aggression and death from worker bees and TI reduced these attacks (Humphreys and Ruxton 2018).

Humphreys and Ruxton (2018), preferring the term TI, defined it as "the unlearned adoption of a motionless posture by a prey individual triggered by physical contact or very close proximity of – not injury inflicted by – a predator (or other antagonist). The posture does not reduce the sensory ability of the predator to locate or identify the prey, or reduce the physical vulnerability of the prey if the attack is pursued. The state of motor inhibition is maintained for a time even after release by the predator, and when in this state the prey exhibits reduced responsiveness to external stimulation (although monitoring of the environment can still occur). In the absence of mortality or injury during TI, the prey can recover its original physiological state on emerging from TI" (p2).

Humphreys and Ruxton (2018) presented a list of confirmed accounts of TI:

- Invertebrates - eg: crustaceans, stick insects, butterflies, beetles, ants and bees.

- Vertebrates - eg: mammals, birds, reptiles, and fish.

The problem, Humphreys and Ruxton (2018) outlined, is "the lack of associated specialist morphological adaptations means that any observer must be present at the moment the behaviour occurs in order to have confidence in its presence in an individual's, or species', defensive repertoire. Even though TI has become co-opted into larger defence strategies in some species, such as aposematic warning or camouflage colouration..., there is no evidence of a strong correlation between TI and traits associated with these other defensive strategies" (p3).

Furthermore, the presence of humans at the moment of predation to observe TI could deter predators, while experiments "in laboratory or otherwise man-made study environments replace — to some extent — practical challenges with ethical challenges of their own" (Humphreys and Ruxton 2018 p3) (appendix 2A). Also the high variability in use of TI within a species adds to the problem of scientifically confirming it (Humphreys and Ruxton 2018).

Humphreys and Ruxton (2018) explained: "As an example, perhaps TI might be more prevalent in snakes because they are generally not especially fleet of movement relative to mammalian and avian predators (reducing the efficacy of fleeing as an alternate anti-predator strategy), and their elongate bodies may facilitate contact by a predator. However, speculations such as this remain no more than 'just so' stories at this stage. We can suggest, though, that because TI requires no anatomical specialisations there seems to be little cost to carrying the potential to use this last-ditch defence when under attack" (p3).

2.2. ANTI-PREDATOR STRATEGY

The predator-prey interaction has been divided into stages, including detection, physical contact, subdue, and consume. Anti-predator strategies have evolved for different stages, but as a "last resort", there is TI (eg: after contact). Humphreys and Ruxton (2018) pointed out: "This makes it quite distinct from immobility used to reduce the risk of predator detection or tracking, since such 'freezing' occurs much earlier in the sequence of a predatory attack. That is, we consider stillness that enhances the effectiveness of camouflage or masquerade to be a different process from TI. Further some animals (eg: pill bugs, armadillos) adopt a curled posture that makes vulnerable body parts inaccessible to predators. We consider this, too, a separate process to TI, which does not rely on making the prey physically less vulnerable to the predator" (p2).

Some vertebrates have feign behaviours including reduced breathing and heart rate, tongue protrusion, and eyes wide open - "features very reminiscent of dead individuals of that species" (Humphreys and Ruxton 2018 p2).

Narayan et al (2013) found the levels of circulating corticosterone in the blood (a stress hormone) correlated with TI behaviours in Fijian ground frogs (Platymantis vitiana). The sight of a predator (cane toad) was enough to induce TI. The frogs were presented with another frog, a toad, a plastic ball or no stimulus for varying degrees of time (figure 2.1).

The common rough woodlice (Porcellio scaber) show the anti-predator strategy of feigning death as studied experimentally [9]. Tuf et al (2015) induced TI in three ways - touch with forceps, squeeze with forceps, and dropping 10 cm. The presence of TI or not was measured,

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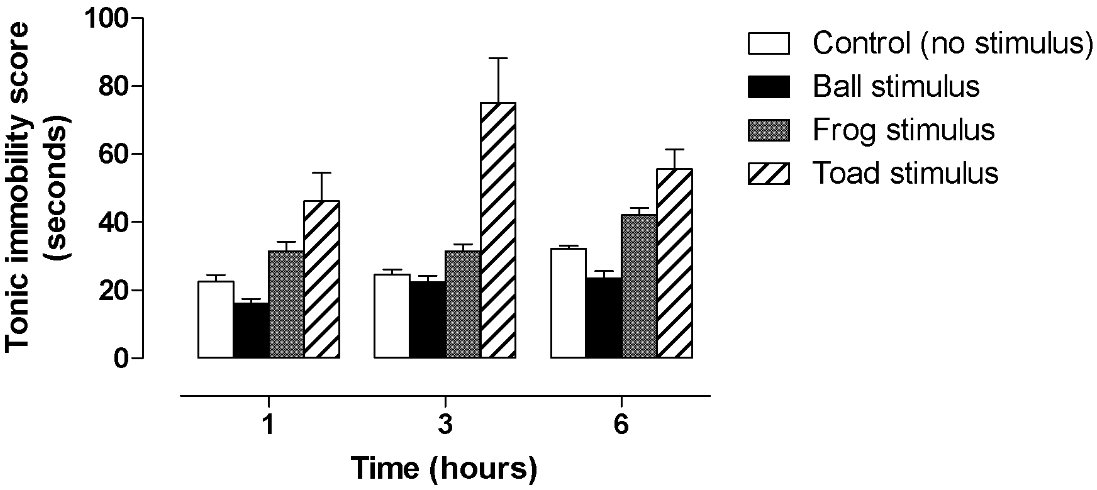
[9] TI is a less common anti-predator strategy than sticking against a surface, running away, or chemical defence (Tuf et al 2015).



(Source: Narayan et al 2013 figure)

Figure 2.1 - Mean duration of TI based on length of exposure to stimulus for Fijian ground frogs.

and its duration if present in five trials for each of the three conditions over three weeks.

Probability of TI, and individual stability of duration of TI across the three conditions were found. Overall, there were significant correlations of TI duration between drop and squeeze, drop and touch, and touch and squeeze.

Some individuals were consistently more bold (ie: shorter TI after stimulus) and some more shy (longer TI).

Edelaar et al (2012) reported individual differences in TI (linked to "boldness") in the yellow-crowned bishop and the tree sparrow. Models of predator birds were placed near the home cages, while the two species of birds were handled and restrained.

TI varies across the life history of the species. For example, one day-old worker red imported fire ants (Solenopsis invicta) respond to worker ants from another nest with TI, but, by one week old, the same workers responded with aggression to aliens (Cassill et al 2008). "In this species, the still-soft exoskeleton of the day-old workers probably renders their ability to inflict damage on alien workers very low, but their vulnerability to damage very high. Hence, TI appears to be the more effective strategy for the earlier fire ant life stage and, indeed, day-old workers were four times more likely to survive such an encounter than week-old individuals encountering similar aliens" (Humphreys and Ruxton 2018 p4).

Pregnant garter snakes were more likely to show TI than non-pregnant females of the same size (Gregory and Gregory 2006).

2.2.1. Explanations

One explanation for feigning death is to use the predator's aversion to long-dead prey (and the risk of toxins). "In this case, TI causes the predator to mistakenly reject a live individual because it is misidentified as a long-dead individual. An implication of this is that the predator must have very simple cognitive functioning in this regard, since the individual that now appears dead was obviously very much alive moments earlier" (Humphreys and Ruxton 2018 p5).

Alternatively, some predators depend upon the prey moving to localise it, and so TI reduces this ability. "This may be at least part of the explanation in cases where prey first drop from a plant to the ground (or otherwise physically distance themselves from a potential predator) ahead of inducing a state of TI. Dropping may hide a prey individual in an underlying, more camouflaging substrate – such as dead leaves or mud – and subsequent stillness would add to the camouflaging effect" (Humphreys and Ruxton 2018 p5). This may also work where many prey are moving and so the predator's attention moves away from the immobile individual.

Honma et al (2006) proposed the explanation that TI involves assuming a posture that makes swallowing whole difficult. This was observed with the pygmy grasshopper that would mean small frogs could not swallow them. "For slightly larger frogs, ultimate swallowing was only possible after time-consuming manipulation to position the immobilised prey correctly in the mouth, hence making eating this prey less attractive from a foraging rate efficiency perspective" (Humphreys and Ruxton 2018 p6). But TI was not shown by grasshoppers with predators that dismember their prey (Humphreys and Ruxton 2018).

Some predators have a hard-wired sequence of actions during prey capture, and TI disrupts this process, which Humphreys and Ruxton (2018) explained, "may cause the predator to break off the attack entirely and abandon the interaction with that particular prey item. However, clearly such maladaptive behaviour from the predator's perspective could only be sustained if the prey concerned were encountered infrequently, such that countermeasures had not evolved. Further, we know of no examples of this being demonstrated" (p6).

Where predators have a limited opportunity with prey as in a group fleeing, Humphreys and Ruxton (2018) explained: "Time spent making sure that one prey item has been immobilised may have an opportunity cost in reduced likelihood of obtaining other prey. Hence, we speculate that it may sometimes be more beneficial to a predator to abandon a prey item that appears immobile or dead in order to take down other prey items while they are abundant before pausing its hunting session to check on its bounty and feed" (p6). This was the explanation preferred by these authors.

Put simply, in a situation where speed to subdue a prey is crucial, the predator will switch prematurely from TI prey, assuming it dead, to catch the next prey. So, TI should be more effective when predators face multiple prey at once with limited time to capture them.

There is evidence to support this prediction from a breeding study by Miyatake et al (2009). Two lines of red flour beetle (Tribolium castaneum) were bred - long and short duration TI. The predator was the Adanson's house jumping spider, who was presented with groups of five beetles (from mixed lines). The predation rate of short TI individuals was 80% compared to 20% for the other line. "TI can still be effective for single prey individuals, if the predator concerned has evolved to release prey quickly, because it often encounters prey in groups, against which quick release can aid in making multiple kills" (Humphreys and Ruxton 2018 p11).

2.2.2. Anti-Predatory Strategy Choice

There are a number of "last ditch" anti-predator strategies including struggling to break free and fleeing, aggression towards the predator, or sacrifice of a minor body part (autotomy). There will be costs and benefits of each of these and of TI. Gyssels and Stoks (2005), for example, found TI by damselfly larvae more likely if the sacrificed body part have been removed previously by the experimenters.

The cost-benefit analysis can also be in evolutionary terms. Ohno and Miyatake (2007) compared TI to flying away in the adzuki bean beetle (Callosobruchus chinensis) by breeding long TI duration individuals together in one line, and short TI duration individuals in another. After a number of generations, the long TI line were found to have weaker flying ability.

In another breeding experiment, with red flour beetles, Nakayama and Miyatake (2010) found that long TI lines experienced less predation, but had less mating success. This was because they were "less active and thus encountering females less frequently: a genetic trade-off clearly exists between an individual's ability to avoid attack and find mates" (Humphreys and Ruxton 2018 p9).

A series of experiments have found that TI vs fleeing depends on the proximity of a place of safety. As the distance to safety is increased, so does the use of

TI (Humphreys and Ruxton 2018) [10].

2.2.3. Crustaceans

Among crustaceans, a freshwater crab (Trichodactylus panoplus) has been observed to show TI (Scarton et al 2009). This animal lives in tidal environments (ie: both in water and on land), and IT is useful when faced with predation risk on land, though risk of dehydration is high (Coutinho et al 2013).

Coutinho et al (2013) reported TI in two freshwater anomuran (freshwater crab) species in South America - Aegla longirostri (AL) [11], and Aegla denticulata denticulata (ADD) [12]. In a laboratory environment, TI was induced by the researchers squeezing the animals gently. AL adults did not show TI, but juveniles did when out of water. This difference may be explained in that the adults are highly aggressive and so fight predators (Coutinho et al 2013).

The ADD were different and showed TI.

The predators of these species use movement to spot prey, so TI is effective in daylight, on land, or where refuge difficult. "Adults of A. longirostri do not seem to need to invest in thanatosis as a defence mechanism, since this species is primarily although not exclusively nocturnal...; its activity rhythm does not always coincide with that of its potential predators... For A. d. denticulata, thanatosis could well serve as a defence mechanism, since this species lives primarily in deeper rivers and does not enter dry environments... This species is often preyed upon by fish, making it advantageous to feign death since there are few refuges, such as rocks, to provide additional protection to these animals..." (Coutinho et al 2013 p2627).

The ADD had a mean TI period of 206 seconds which is longer than other crustaceans studied (eg: 33 seconds; Scarton et al 2009).

2.3. APPENDIX 2A - TWO CLASSIC STUDIES VIEWED AS ETHICALLY CHALLENGING TODAY

Sargeant and Eberhardt (1975) reported their tests in 1971 with five species of duck and their predator, the red fox. Groups of 1-4 or 4-10 ducks were released into a pen along with a fox. The reaction of the ducks was

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[10] Anti-predatory strategy chosen can depend on the predator (appendix 2B).

[11] Live in streams in Southern Brazil, but do venture on to land sometimes at night. More details at http://tolweb.org/Aegla_longirostri/76246.

[12] Live in deep streams in Chile. More details at http://tolweb.org/Aegla_denticulata_denticulata/76296.

observed. Some ducks that were attacked were removed, but others were not. In total, the capture and handling by the foxes of approximately fifty ducks was observed.

The ducks tried to escape, but when seized, 29 showed TI. The length of TI varied from 20 seconds to fourteen minutes (with a mean of four minutes). "Death-feigning ducks appeared alert and aware of escape opportunities" (Sargeant and Eberhardt 1975 p111).

Sargeant and Eberhardt (1975) described one episode which showed the advantage to the duck of TI: "An adult male fox attacked two female mallards standing on a gravelled roadway in the pen. The fox seized one and the bird death-feigned immediately. The fox then walked about 15 m, and laid the bird down. After mouthing it, he started back toward the second bird, but turned and saw the first bird escaping, He ran back, recaptured it, and the bird death-feigned again. The fox laid it down again at the same site, mouthed it, and began walking back toward the second bird. Midway between the two birds he turned and saw the first bird escaping again. The fox hesitated, but this time attacked and, captured the second bird. The first bird escaped to the pond" (pp113-114).

Overall, "ducks had a better chance to survive capture if they death-feigned rather than struggled... [so] immobility minimised stimulation for further attack" (Sargeant and Eberhardt 1975 p116).

The researchers continued: "Captured birds, however, survived largely because of the relatively gentle prey-handling characteristics of the foxes, and, therefore, death-feigning after capture would be ineffective as a survival mechanism against predators that kill or cripple prey immediately" (Sargeant and Eberhardt 1975 p116).

Francq (1969) studied TI in common opossums (Didelphis marsupialis) (figure 2.2) by grabbing and shaking the animals, or using a dog to do so. A highly stereotyped behaviour pattern was observed - "the animal would 'freeze' momentarily with its head pointed straight ahead. It then flexed ventrally by bending the head toward the chest, contracting the abdominal and ventral tail muscles, and fell onto its side. At times the tail was curled between the hind legs. The corners of the mouth were drawn back simultaneously with the flexure and the tongue often extended either between the incisors or out one side of the mouth. The digits of the forefeet were flexed and the animal would grab pieces of grass, leaves or other material on which it was lying and hold on with some tenacity when lifted. The eyes remained open though usually not so, widely as when the animal was normal" (Francq 1969 pp557-558).

(Source: Kueller - American Museum of Natural History, New York 2011)

Figure 2.2 - Taxidermy model of common opossum.

Compared to sleep, the eyes and mouth were open, the ears twitched to sharp sounds, and there was no arousal when prodded (Francq 1969).

2.4. APPENDIX 2B - ANTS CHOOSE ANTI-PREDATOR STRATEGY WITH SNAKES

Eusocial insects like ants show "surprisingly variable and complex co-operative behaviours", particularly the non-reproductive (or "less-reproductive") castes (Jono et al 2019).

Anti-predator defence is one such behaviour, including biting, stinging, venom spraying, and self-destruction. Jono et al (2019) studied the case of an ant in Madagascar (Aphaenogaster swammerdami [13]) and a large blindsnake predator (Mocquard's worm snake; Madatyphlops decorsei).

Ant colonies were tested experimentally with this snake, another snake that predates on snakes and vertebrates (Madagascarophis colubrinus), and a frog-eating snake (lateral water snake; Thamnosophis

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[13] Image and information at http://www.antweb.org/bigPicture.do?name=casent0017663&number=1&shot=p.

lateralis).

Upon the presentation of the Mocquard's worm snake, the worker ants ran into the nest and co-operatively evacuated pupae and larvae, but not with the other two snakes. This was a temporary relocation only. There was an aggressive reaction to the lateral water snake (eg: biting), but the M colubrinus was allowed into the nest.

These are two specialist anti-predator tactics which show evidence of recognition of different snake species. The removal of pupae and larvae when the Mocquard's worm snake was nearby because it feeds on them, and allowing the M colubrinus into the nest as it feeds on other snakes and vertebrates that predate the ants rather than pupae and larvae.

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3. LEARNING AND FLEXIBILITY

3.1. LEARNING

The term "life history" is used in relation to evolution to refer to "the developmental programme of an organism, including its period of immaturity, reproductive rate and timing, caregiving investment and longevity" (Gopnik et al 2020 p1).

Learning in childhood is costly in evolutionary terms - eg: energetically expensive brain; greater predation risk with exploration. Snell-Rood and Snell-Rood (2020) proposed the "developmental support hypothesis" that argues that "young mammals should invest in learning, and bear its associated costs, to the extent that they receive sufficient nutritional and protective support from their parents. Without such support, juveniles have fewer resources and are exposed to greater risk. In that case, it might be adaptive to develop a phenotype that learns and explores less, but is also less costly and risky, and improves the chance of survival in difficult conditions" (Gopnik et al 2020 p2).

Uomini et al (2020) provided some support for this idea in work with Siberian jays and New Caledonian crows, who have an extended juvenile period of receiving parental care. "Although these birds do not engage in the kinds of sophisticated cultural and social learning we see in humans, parents nevertheless provide a tolerant environment that allows the young to develop distinctive cognitive skills. Moreover, the young New Caledonian crows are able to engage in extensive active exploration and trial and error learning during this period, even with little immediate benefit or reward" (Gopnik et al 2020 p3).

The complexity of the early environment is also important. Rojas-Ferrer and Morand-Ferron's (2020) work with captive zebra finches found that the highest learning ability developed in early environments that presented "a moderate amount of information; not too little or too much" (Gopnik et al 2020 p2).

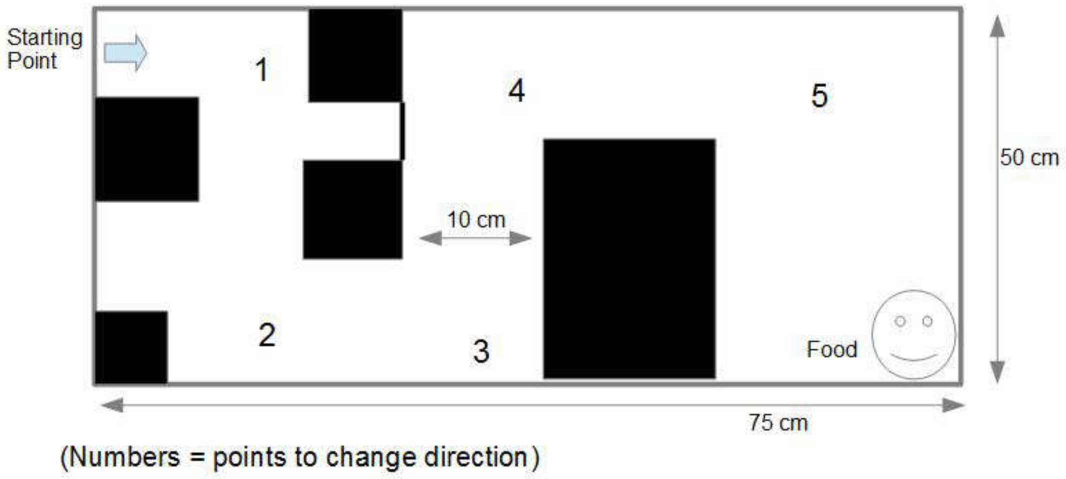
Gopnik (2020) talked of two types of cognition - exploration and exploitation. The former is "the ability to search through a wide space of possible hypotheses, actions or problems solutions" (in the language of computer science and neuroscience), while the latter is "the ability to use those hypotheses, actions and solutions to bring about desirable and useful outcomes" (Gopnik et al 2020 p3). Gopnik et al (2020) continued: "Exploration may benefit from variability, impulsivity and intrinsically driven curiosity and neophilia, for example, whereas exploitation requires focused capacities for executive function and long-term planning" (p3).

Gopnik (2020) found that human children can outperform adults on tasks using exploration cognition, and this ability benefits from parental support that makes exploration possible. Perry (2020) found a similar pattern among wild white-faced capuchins and foraging (eg: younger individuals more creative) (Gopnik et al 2020).

3.2. CRABS AND SPATIAL LEARNING

Spatial learning is viewed as a more complex form of learning, and has "so far been demonstrated in only vertebrates and a select number of invertebrate species" (Davies et al 2019 p1). Davies et al (2019) considered crustaceans (who have less neurons in the brain than insects that show spatial learning - eg: honey bees one million vs 90 000 neurons in a crayfish brain), and, in particular, the European shore crab (Carcinus maenas).

These crabs inhabit inter-tidal and shallow sea ecosystems, and twelve of them collected in South Wales were tested in an experimental maze. "The maze had a single correct path to the endpoint, requiring five changes of direction and included three dead ends. All passages were 10 cm wide and a direct route from the starting box to the endpoint required the crabs to traverse ca 2 m" (Davies et al 2019 p2) (figure 3.1). The crabs were trained on the same day weekly for four weeks (ie: food at the end of the maze), and tested two weeks later (ie: no food). The time to complete the maze (latency) was measured, and the number of wrong turns.



(Based on Davies et al 2019 figure 1a p2).

Figure 3.1 - Drawing of experimental maze.

The average time to complete the maze was 25 minutes during training, and, along with the number of wrong turns, this declined each time, especially after week 3. The time was eight minutes in the test. Control crabs (ie: with no training or food at the end of the maze) showed no evidence of learning.

In summary, "[C]rabs showed a strong capacity for spatial learning over the timescale of this work" (Davies et al 2019 p3).

But the "potential for allocentric (the use of landmarks) learning cannot be entirely discarded; however, as crabs may have used the position of the camera or other overhead features" (Davies et al 2019 p3). The position of the food and the shape of the maze were not changed during training.

It is also possible that the crabs used sequential learning rather than spatial learning - ie: "right turn, ignore two openings, left turn, left turn, right turn, right turn" (Davies et al 2019 p3).

3.3. SOCIAL INFORMATION

When faced with potential prey, predators must make a decision to attack or avoid. The former is linked to "profitability" (eg: nutrient content), and the latter to costs (eg: palatability). Predators acquire information from direct past encounters to help in this decision, and indirectly via social information (eg: observing other individuals). Social information about prey defences produces "social avoidance learning", and it is "assumed to be beneficial for predators, as it can reduce the time and energy invested in prey sampling, as well as the potential costs for consuming toxic prey" (Hamalainen et al 2020 p1154).

Who can provide social information? Individuals from the own species (conspecifics), of course, but also heterospecifics (those from another similar species who eat the same prey) (table 3.1).

Social avoidance learning may be a selection pressure on aposematic prey (ie: conspicuous warning colouration of unpalatability) (Hamalainen et al 2020).

Study	Details
LeFebvre et al (1997)	Carib grackles copy zenaida dove "tutor's" foraging techniques
May & Reboreda (2005)	Shiny cowbirds copy screaming cowbirds on novel foraging task

Table 3.1 - Two experimental studies showing heterospecific social information in birds.

Great tits (Parus major) and blue tits (Cyanistes coeruleus) form mixed foraging flocks, which allowed Hamalainen et al (2020) to study conspecific and heterospecific social avoidance learning in an experiment in Finland.

Almond flakes were used as the novel prey, and the unpalatable pieces were soaked in a bitter-tasting solution and marked with a conspicuous square symbol. Palatable flakes were marked with a cross symbol, and made cryptic (within cross symbols). In other words, it was easier to see the unpalatable food.

Individual birds were shown a video of a conspecific or heterospecific "demonstrator" bird foraging the unpalatable flakes and showing a disgust response (wiping their beak on their perch and shaking their head) (or no information) before being given the opportunity to forage. Twelve birds of each species were assigned to each of the three conditions. The number of aposematic prey handled or consumed was the dependent variable measure.

It was found that the "birds handled and consumed fewer aposematic prey after receiving either conspecific or heterospecific information" (Hamalainen et al 2020 p1159). The effect was stronger in blue tits compared to greet tits, and "blue tits also learned more efficiently from watching conspecifics, whereas great tits learned similarly regardless of the demonstrator species" (Hamalainen et al 2020 p1153).

3.4. TOOL USE

3.4.1. Dolphins

Differences in behaviours between social groups or populations of the same species have three possible explanations, in the main (Wild et al 2019):

i) "Cultural hypothesis" - Social learning and transmission of behavioural innovations.

ii) " Ecological hypothesis" - The behaviour is a product of specific environmental/ecological pressures.

iii) "Genetic hypothesis" - Inheritance.

These explanations are not mutually exclusive, as well as there being other possible explanations (Laland and Janik 2006).

Behavioural innovations in a group or population are interesting, like "sponging" by Indo-Pacific bottlenose dolphins (Tursiops aduncus) in Shark Bay, Western Australia. "This behaviour involves dolphins carrying conical sponges as protective 'gloves' on their rostra when foraging for buried prey" (Wild et al 2019 p2).

Wild et al (2019) made observations of dolphins using "sponging" in 2017 and 2018. Overall, 76 individuals were identified as "spongers" (of which forty-nine were female). Where data were available, all "spongers" were born to "sponging" mothers.

In explaining the "sponging" behaviour, Wild et al (2019) dismissed the "ecological hypothesis" because "the deep-water channels where sponging occurs were used by both 'spongers' and 'non-spongers'..." (p2). The "genetic hypothesis" would expect the "sponging" individuals to be closely related, but the dolphins studied were not more closely related than expected by chance. This left the "cultural hypothesis" - in the form of vertical social transmission of "sponging" from mother to (primarily female) offspring (ie: matrilineally).

However, Wild et al's (2019) explanation was a bit more complex. "Sponging" offspring learned the behaviour, and carried particular genes. This has been called "cultural hitch-hiking" (Kopps et al 2014) - "a form of gene-culture co-evolution in which a neutral genetic locus is inherited in parallel with a matrilineally transmitted cultural behaviour" (Wild et al 2019 p4).

Wild et al (2020) described another interesting behaviour by dolphins in the same area using large marine gastropod shells - "shelling". "Dolphins utilise the shell to first entrap the prey before exposing it to gravity by lifting the shell above the water surface and shaking it about in order to dislodge the prey, thereby fulfilling these conditions and qualifying shelling as tool use" (Wild et al 2020 p3027).

A total of 42 shelling events by nineteen individuals were observed between 2007 and 2018. Based on the individuals showing the behaviour, the researchers believed that shelling was an example of social learning by unrelated (but associating) individuals (horizontal social transmission).

3.4.2. Chimpanzees

Two aspects of tool-use by wild chimpanzees has been studied - the form and frequency of the behaviour. "The form of a behaviour can be defined as the action components involved in the behaviour (which can be organised in both a linear and/or hierarchical relationship). The frequency of the behaviour is the rate of occurrence of a behavioural form within and across populations" (Bandini and Tennie 2019 p2).

The "form-copying hypothesis" describes one individual in a group showing an innovative behaviour, and others then copying it (eg: Whiten et al 1999). "The behavioural form becomes a population-wide variant once a sufficient number of individuals have copied the innovation. The regional differences in the behavioural repertoires observed across chimpanzee populations... are then attributed to independent individuals in the past having innovated different behavioural forms that were then transmitted to the rest of the population via high-fidelity social learning mechanisms [eg: imitation]" (Bandini and Tennie 2019 p2).

Bandini and Tennie (2019) questioned the "form-copying hypothesis". They referred to archaeological evidence for 4000 years ago of nut-cracking by wild chimpanzees in the Tai Forest (Mercader et al 2002), which showed a general form of tool use unchanged. "If this behaviour were transmitted solely via social learning, then through copying error alone (which is unavoidable when copying behaviours...), we would expect to see changes in the form of the behaviour" (Bandini and Tennie 2019 p2).

Bandini and Tennie (2017) proposed the alternative idea of "socially-mediated serial reinnovations" (SMSR). Also known as the "zone of latent solutions hypothesis" (ZLS) (Tennie et al 2009). The "behavioural forms increase in frequency in populations due to low-fidelity social learning [eg: stimulus enhancement or "latent solutions"] helping others reinnovate the behaviour on their own. The resulting behavioural forms therefore derive individually, and do not need to be copied" (Bandini and Tennie 2019 p3).

The ZLS hypothesis is counter to the form-copying hypothesis" because "instead of assuming that great apes have enhanced social learning skills as compared to many other animals, the ZLS hypothesis implies instead that their innovation skills that are enhanced" (Bandini and Tennie 2019 p3).

Bandini and Tennie (2019) tested the ZLS hypothesis by providing naive captive chimpanzees with the material that could be used to solve a problem. In this case, "stick pounding" was the solution - ie: "the use of a tool with a pounding action to mash a desirable food in a cavity, so that it can be retrieved" (Bandini and Tennie 2019 p4). A hard-boiled potato was placed in a container with a hole, and it could be removed by pounding into smaller pieces. Sticks were available in the cage.

Four groups of chimpanzees at a wildlife orphanage in Zambia were tested. In three of these groups, one individual spontaneously used "stick pounding" to get the food. Subsequently, 14% of other individuals in the groups acquired the behaviour. More chimpanzees in the group would be expected to show the behaviour over the six weeks of the study if imitation was at work.

In another study, Motes-Rodrigo et al (2019) found that captive chimpanzees could use sticks to dig up food without having seen the behaviour before (appendix 3A).

These examples "may help explain why our hominin ancestors kept making the same simple tools for millions of years. Like chimp, they might have repeatedly reinvented certain tools, but struggled to learn improvements from others" (Marshall 2019 p11).

The elements of tool use can vary between different groups. For example, Boesch et al (2020) compared 39 wild chimpanzee communities for "termite fishing" (inserting a stick into a termite mound to get the termites). Ten of the groups showed the behaviour, and based on an analysis of the behaviour, 38 elements were distinguished. "Individuals in the same community used more similar techniques compared with chimpanzees from other groups. In other words, there were local cultural differences... It seems that the differences aren't functional, in that some methods work better in one place than another, but cultural, and that chimps moving to a new community change their methods to fit in with their new social group and hasten social acceptance and integration" (Hooper 2020 p17).

3.5. PERFECTING SONGS

Male sexually selected characteristics are a product of male-male competition and female choice. Bird song is an example of this. "Males of most songbird species (oscines) that breed in the temperate zone sing intensively during the breeding period to repel rivals and to attract females. The singing performance of male individuals is thus a crucial component in estimating their quality for both competitors and potential partners" (Souriau et al 2019 p2).

Souriau et al (2019) wondered why males would sing outside the breeding season, particularly among migrants at their wintering grounds. One answer is as territorial defence, but the evidence between species varies (eg: territorial defence in the marsh warbler, but not the willow warbler) (Souriau et al 2019).

Alternatively, Sorensen et al (2016) proposed the "song improvement hypothesis", which stated that "practicing complex songs during the non-breeding season could improve song performance for the following breeding season, and thus positively impact individual fitness" (Souriau et al 2019 p2). This makes sense because the song of songbirds is a learned behaviour, which young birds perfect from listening to adults.

Souriau et al (2019) tested this idea with thrush nightingales (Luscinia luscinia), who were recorded singing during the breeding season in Poland in 2009 and Russia in 2012 and 2013, and in the wintering grounds in Tanzania in 2006. The songs were analysed by spectrogram for individual syllable consistency, and element variability [14].

Songs recorded in Tanzania were "poorer quality" (ie: lower syllable consistency and higher element variability) than during the breeding season. Consistency is highly prized by females. The researchers believed that the wintering songs represented practice or improvement by older males (ie: vocal plasticity, which is usually assumed among juveniles only), and supports the "song improvement hypothesis".

There is another explanation for the wintering songs, namely the "market place hypothesis" (Kipper et al 2017). This proposes that "singing outside of the breeding season could be an opportunity for older birds to learn and share new songs with nearby wintering individuals. Wintering grounds would then constitute a song 'market place' where males would go through a new sensory phase of song learning, allowing better territorial communication with neighbouring conspecifics over time. From this point of view, the 'market place' hypothesis can be regarded as a part of the song improvement hypothesis" (Souriau et al 2019 p12).

The recordings of the songs were made

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[14] A syllable is a sound that is always repeated in the same sequential order, and three types of syllables were distinguished. Elements are the different types of sounds (eg: "castanet" ending) (Souriau et al 2019).

opportunistically, and there was no information on the age or pairing status of the birds. Recordings of the same individuals at both sites would be the ideal.

Support for the "song improvement hypothesis" has been found in bird species including Blyth's reed warblers and common nightingales (Souriau et al 2019).

3.5.1. White-Throated Sparrows

There is over fifty years of recordings of the songs of the male white-throated sparrow (Zonotrichia albicolis) in North America. The traditional song is a whistle ending in repeated triplets of notes (recorded in the 1960s; eg: Borror and Gunn 1965). This is being replaced by a doublet ending (ie: a different "dialect") (Otter et al 2020).

Otter et al (2020) analysed 1785 recordings from 2000 to 2019 to show the spreading of the doublet ending from British Columbia, Canada, to most of the country. "As of 2019, the doublet-ending song variant appears to have spread completely across the western portion of the species' geographic range, with all birds singing doublet-ending songs, while only the eastern portion of the range has retained the triplet-ending song variant" (Otter et al 2020 p3232).

At the Algonquin Park Research Station, Ontario, for example, long-term data were available. In 2005, 1 of 76 males sampled (1.3%) produced the doublet ending song compared to 49% of 92 males sampled in 2017 (Otter et al 2020).

Geolocation data have shown that birds with the different "dialects" overwinter together, and "the spread of song variants among populations may be facilitated by song tutoring on the wintering grounds" (Otter et al 2020 pp3232-3233).

Males do not appear to differentiate between the two songs in terms of territorial response, so Otter et al (2020) asked why did the song change so quickly? One theory that can be applied is the "indirect biased transmission hypothesis" (Trainer 1989), which "suggests that certain innovations in song are non-randomly adopted by males within a population, leading to fast population-level transitions to new song variants" (Otter et al 2020 p3233). Juvenile males are willing to change their songs because females pay attention to the terminal portion of the song, and "males may integrate novelty to maintain female interest" (Otter et al 2020 p3233).

3.5.2. Genetic-Environment Interaction

Work with songbirds has shown the interaction of genes and environment in learning song dialects. For example, birds raised hearing only song playbacks have a tempo to their song strongly influenced by their genes (Mets and Brainard 2018), but genes are less influential for the tempo of songs of young birds raised with an adult (Chen et al 2016).

Mets and Brainard (2019) used the Bengalese finch (Lonchura striata domestica) in developing this research. The song of young birds raised by their own parents were learnt bettern than by birds from eggs placed in fostered nests before hatching. This suggested that "a match in genetic propensity for learning is key to how well birds learn songs" (Tchernichovski and Conley 2019 p290).

But adoptive birds learnt well if the tempo of the song they heard was similar to their own because "[I]t seems that certain birds are genetically tuned to learn and produce slow songs, whereas others are wired for fast songs" (Tchernichovski and Conley 2019 p291). This was confirmed using a computer-based synthetic song. The tempo of the synthetic song matched to the genetic predisposition of the young bird led to better learning. The genetic predisposition of tempo was established from the bird's biological father (Tchernichovski and Conley 2019).

3.6. FROGS

3.6.1. Rapid Evolution

An invasive predator (ie: new to a ecosystem) can dramatically reduce a native prey, but, if extinction does not occur, the survivors are non-random, "there is a potential for rapid adaptive evolution" (Komine et al 2020 p126).

Islands are "natural laboratories" for these processes. Examples of extinction on islands include the Lord Howe starling (Aplonis fusca) after the arrival of rats, and the Chatham island bellbird (Anthornis melanocephala) also from rats (and cats) (Komine et al 2020).

Komine et al (2020) reported a case of rapid evolution on Amami Island (Nansei Islands, southern Japan), where Indian mongooses (Herpestes auropunctatus) was the invasive predator in the northern part of the island (after 1979). An eradication programme initiated by the Japanese government removed all mongooses (after 2000).

Rapid evolution could be observed in behaviours in a species exposed to the invasive predator compared to those not exposed. In this case, the Amami tip-nosed frog (Odorrana amamiensis) (figure 3.2) and flight initiation distance (FID). Here "the distance at which an animal begins to flee from an approaching potential predator, is widely known as an index of sensitivity to predator attack... When predation pressure by an invasive mongoose is strong, it could increase the FID of native species in the area where the mongoose has been established for a longer period" (Komine et al 2020 p127).

(Source: Hi-tanio)

Figure 3.2 - Amami tip-nosed frog.

When the researchers detected a frog, one of them walked at a constant speed towards it, and recorded the distance at which the frog initiated its escape behaviour. Data were collected on 278 frogs in mid-2013. It was found that "the native frog became more sensitive to the approach of a potential predator as the historical impact of the mongoose increased, suggesting that past strong predation pressure by the mongoose drove a rapid behavioural response in the native frog" (Komine et al 2020 p126). For example, frogs had a mean FID of 323 cm in areas of the island where mongooses had been common compared to 143 cm in other areas of the island. Small and medium-sized frogs were more sensitive to the approach of the researcher than large frogs.

Komine et al (2020) noted that "even if a decline in the population of an invasive predator results in the recovery of a native prey population, rapid behavioural responses of the native prey remain" (p131).

The researchers believed that the frogs they tested would rarely have experienced actual mongoose attack, and so the behaviour change can be assumed as evolved rather than learned by individuals in their lifetime.

3.6.2. Call Changes

Humans have impacted the natural world in many ways, including through the growth of towns and cities. "Urbanisation is likely to impose strong selection on animal communication, as effective production, transmission and perception of signals is heavily influenced by environmental conditions, such as differences in noise or light pollution, or food availability. Urbanisation may also affect the abundance of predators and parasites that tune in on communication signals, thereby indirectly altering the selection pressures that operate on signallers. Given the divergent selection regimes, it is not surprising that urban animals often sound, look and behave differently compared to their non-urban conspecifics" (Halfwerk et al 2019 p374).

Halfwerk et al (2019) studied the tungara frog (Physalaemus pustulosus) in this context. In the rainy season, males gather at night in puddles to call to females. Complex calls are most attractive. "Sexual selection for these more elaborate displays is, however, counterbalanced by natural selection imposed by predators and parasites, as bats and midges also preferentially attack males that produce more complex calls. Notably, the communication system of the tungara frog is affected by conditions that are associated with increased urbanisation" (Halfwerk et al 2019 p374).

Calls were recorded in Panama in 2016 and 2018 in urban and forest areas (field recordings). Females from urban and rural areas were tested in the laboratory with a choice of two calls (mate choice experiment). Also selected males from urban and rural areas were swapped over (translocation experiment).

The field recordings showed differences between the urban and rural frogs. Forest males ceased calling quicker when a human approached (mean 4.5 m away vs 2.5 m), but their calls were at a lower rate (mean 25 vs 28 calls per minute) and less complex than urban frogs [15].

In the mate choice experiments, where a urban frog call was played on one loudspeaker and a rural call on the other speaker, 30 of 40 females approached the speaker with the urban call. In the translocation experiment, urban males were better able to adjust their calls (ie: reduced call complexity).

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[15] Call rate was defined as number of calls per minute, and complexity as number of "chucks" per call.

Halfwerk et al (2019) explained the differences in call complexity as "related to differences in the selection pressures imposed on the signallers in both environments; urban males experienced more competition for mates, but had a lower risk of predation and parasitism compared to forest males" (p376). They continued: "Our data suggest that these urban phenotypes have a reproductive advantage over the forest phenotypes in urban areas, whereas in forest areas none of the phenotypes has an advantage in terms of mate attraction, or predator and parasite avoidance. The most important driver of this selective advantage seems to be the absence of predators. Predators tend to be the first species that disappear from polluted or fragmented sites, which would suggest that urban males also out-compete forest males in degraded forest habitats" (Halfwerk et al 2019 p377).

3.7. NEUROGENESIS

The growth of new cells in the adult brain (neurogenesis) is debated as to the "precise functional significance" in different species (Dunlap et al 2019). A well-known example is the seasonal changes in day length and neurogenesis of cells in the brain areas related to singing ("song nuclei"), and seasonal song production in some bird species (Dunlap et al 2019).

Dunlap et al (2019) explained: "Most of our understanding of environmental influences on adult neurogenesis comes from laboratory studies in which researchers manipulate environmental stimuli and document effects over the timescale of days to months. That is, they demonstrate an external factor driving phenotypic plasticity in the neurogenic rate. However, the neurogenic rate can also be influenced by intrinsic genetic factors, and thus, over evolutionary timescales, the environment can modify the neurogenic rate via natural selection acting within populations. Selection could act directly on the neurogenic rate if enhanced (or reduced) brain plasticity confers an advantage in responding to environmental change" (p1).

There are three possible ways that this could happen, according to these researchers:

i) Phenotopic plasticity - An aspect of the environment leads to neurogenesis, which in turn leads to behaviour change in the individual. For example, particular odours in the environment trigger neurogenesis in the olfactory bulb of rodents, and this leads to enhanced odour discrimination abilities (Dunlap et al 2019).

ii) Direct selection on the brain - Selection pressure of the environment on a particular behaviour, which alters the brain, and this produces an adaptive behaviour.

iii) Selection pressure on life history - Selection pressures leads to altered investment in brain growth, and subsequently to adaptive behaviours.

Dunlap et al (2019) studied the male Trinidadian killfish (Rivulus hartii) with reference to these three possibilities. Populations of the fish in Trinidad live in rivers with no predations (Rivulus only (RO) sites) or exposed to predatory fish (low predation (LP) or high predation (HP) sites) [16]. Fishes captured at different sites were kept in laboratory environments, and breeding experiments were performed ("common garden experiments").

"Wild-caught fish from HP sites had brains with significantly higher mean proliferating cell density in all brain regions (approx. two-fold higher) than fish from sites with no (RO) or few (LP) predators" (Dunlap et al 2019 p4). These differences persisted even in first generation laboratory-bred fish who lived with the absence of predators. "These results strongly indicate that population-level differences in cell proliferation in males are driven at least partially by natural selection, with predators selecting for genetic mechanisms that also enhance the cell proliferation rate" (Dunlap et al 2019 p6).

This makes sense for cell proliferation in areas of the brain linked to anti-predator behaviour, but other areas of the brain also grew more in the HP-site fish. The researchers were not sure here, and recommended more research.

3.8. SHARKS

Sharks have existed for over 400 million years in some form, and have survived mass extinctions that wiped out other animals. What are the qualities of these fish with a cartilaginous skeleton that have aided survival?

One answer is a highly efficient digestive system that processes almost all of its food (as observed by their faeces being a "clearish goo" with few solids). This is helpful when food is scarce (Joel 2019).

Related to this is the ability to eat anything (omnivorous) - not only different prey types, but some species of shark eat seagrass and shellfish (Joel 2019).

There is evidence that ancestors survived in saltier

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[16] Predators (eg: wolf fish; Trinidadian pike cichlid) are 10-50 times bigger, and the probability of surviving an attack is low. Thus, selection pressure on behaviours that increase the avoidance of predators (eg: via brain growth).

water, and in hotter oceans. So, flexibility is another key characteristic of shark species (Joel 2019).

However, overfishing has played a role in the current situation where about one-sixth of shark species are listed as threatened (Joel 2019).

3.9. OBJECT RECOGNITION

Newport et al (2018) began: "Object recognition is fundamental to many complex visual behaviours (eg: food detection, mate selection, individual recognition) and yet it is a far from trivial task because changes in viewing conditions (eg: lighting or viewing direction) can drastically alter the two-dimensional (2D) image cast in the eye of the observer by the three-dimensional (3D) object" (p39).

A recognition system that is swift and requires less processing power will be inflexible, and best at view-invariant recognition (ie: can recognise an object from one angle only) (appendix 3B). On the other hand, a more flexible recognition system would allow the animal to recognise objects from novel viewpoints, but it is slower and more demanding of cognitive processing power.

Studies have used the human face as the object to recognise. For example, Dyer and Vuong (2008) trained honeybees to discriminate between two faces (frontal view), and later presented the faces at different angles. There was some recognition (Newport et al 2018).

Newport et al (2018) used this method with six archerfish (Toxotes chatareus). Using a pair of pictures of the frontal view of a human face, spurting a jet of water at the correct one on a computer screen led to a food pellet reward.

In the testing phase, the familiar faces were presented at three novel orientations (30°, 60°, and 90°).

There were individual differences, but generally the fish could recognise the faces at all three novel rotations. The fish did take longer to respond when the face was rotated. Newport et al (2018) commented: "The observed increase in response time suggests there may be a cost in performance as the appearance of the faces becomes increasingly different from the exemplar. In a laboratory setting where decision time does not impact the quality of the food reward, it makes sense to take the time to make a correct decision, but recognition requiring extended decision time is unlikely to be practicable for archerfish in natural conditions where interspecific competition for food is intense and catching prey quickly is imperative to avoid theft" (p44).

3.10. APPENDIX 3A - MOTES-RODRIGO ET AL (2019)

Plant underground storage organs (USOs) (eg: tubers) are believed to have been important to hominins as a food source, as they are to some monkeys. Shallow USOs can be excavated by hand, but tool-use makes the process easier and aids in excavating deeper ones. Observations of tool-use by wild chimpanzees here are sparse (Motes-Rodrigo et al 2019).

Two captive primate species, however, have been tested experimentally:

a) Tufted capuchins used sticks to excavate peanuts buried in soil (Westergaard and Suomi 1995).

b) Bonobos used branches to excavate food buried below two layers of sand and stones (Roffman et al 2015).

Motes-Rodrigo et al (2019) tested captive chimpanzees at a zoo in Norway (n = 10) in two experiments (figure 3.3).

Experiment 1

This investigated three questions: "i) whether and how the chimpanzees would use tools to excavate buried food, ii) if soil compactness would influence tool use excavation, and iii) if chimpanzees would be selective in their choice of tools" (Motes-Rodrigo et al 2019 p3).

The chimpanzees were provided with sticks (ready-made tools) (figure 3.4) to help in excavating food. In the "open hole condition" (OH1) (control), food was placed in five holes (each 30 cm deep). There were two conditions where the food was covered - "loose soil condition" (LS1) (non-compacted soil) and the "compacted clay condition" (CC1). The whole experiment lasted 66 days and was videotaped.

None chimpanzees used manual excavation when the food was buried, and seven of them employed tools [17]. Six types of behaviour using sticks were observed - probe (most common in LS1), perforate, pound, shovel, dig (most common in CC1), and enlarge (figure 3.5; table 3.2). The compactness of the soil had no effect on tool use frequency.

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[17] Note that no guidance or demonstration was given to the chimpanzees.

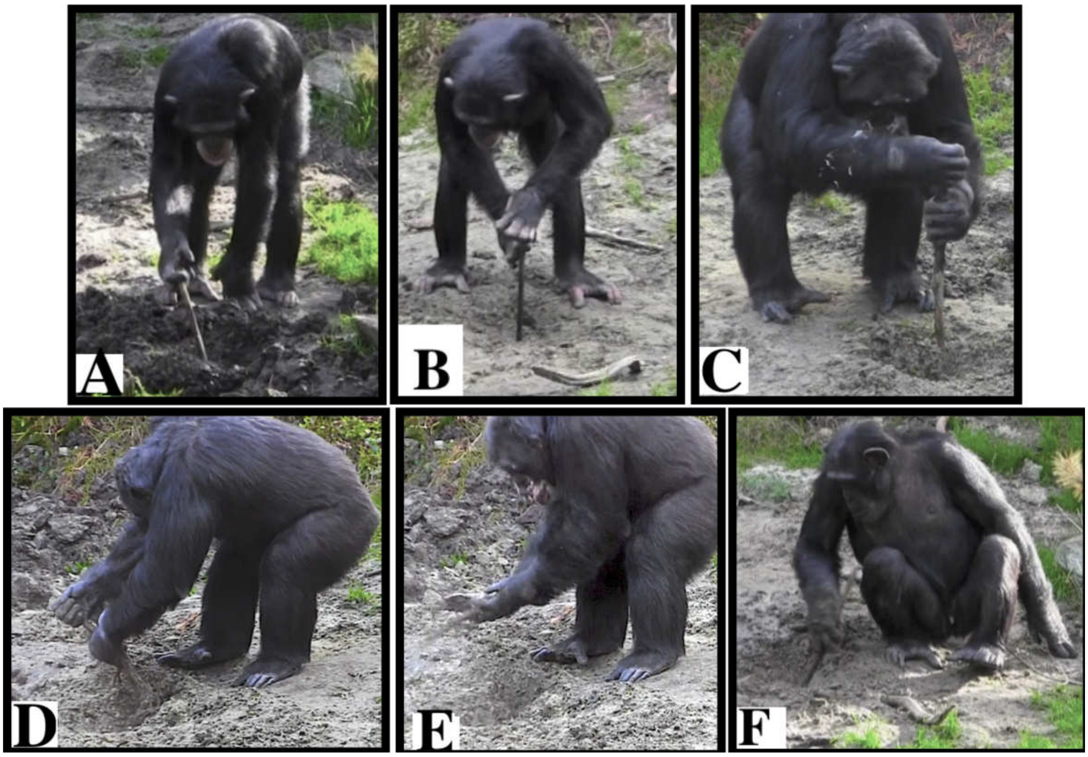
(Yellow lines indicate area used in Experiment 1 and red lines Experiment 2)

(Source: Motes-Rodrigo et al 2019 figure 1)

Figure 3.3 - Photographs of chimpanzees' enclosure.

(Source: Motes-Rodrigo et al 2019 figure 2)

Figure 3.4 - Sample of tools provided in Experiment 1.



(Source: Motes-Rodrigo et al 2019 figure 3)

Figure 3.5 - Photographs of different tool use behaviours - (A) probe, (B) perforate, (C) pound, (D) dig, (E) shovel, and (F) enlarge.

Experiment 2

This investigated manual versus tool excavation, and no tools were provided by the researchers. There was only the "open hold condition" (OH2) and "compacted soil condition" (CS2). In the latter condition, only 10% of occasions involved tools.

Figure 3.6 shows the proportions of different behaviours in both experiments.

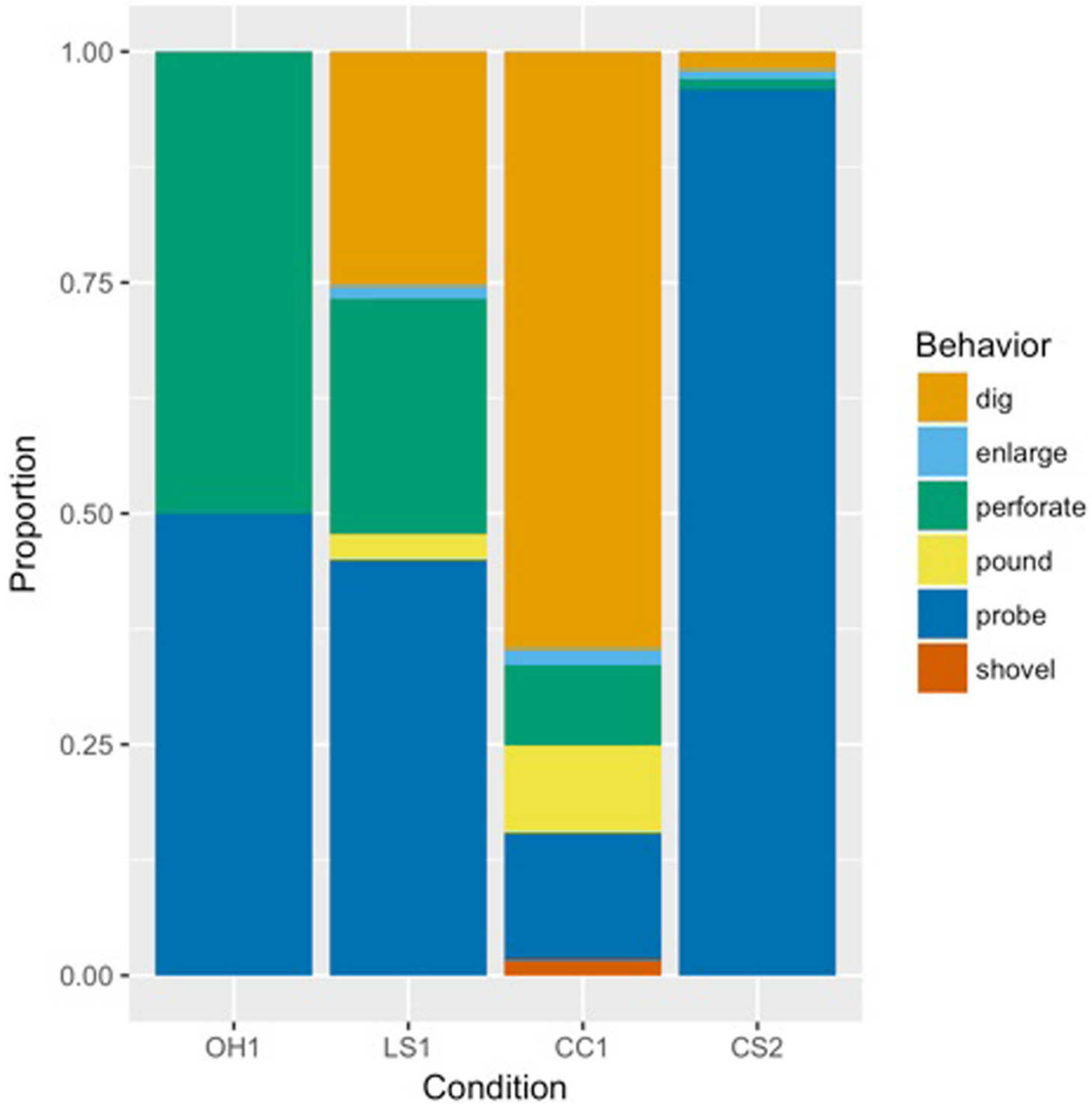
Motes-Rodrigo et al (2019) summarised their findings: "Our results demonstrate, for the first time, that excavating-naïve chimpanzees are able to spontaneously use tools in order to excavate artificially buried food. Further, the majority of individuals in our study succeeded in excavating with tools. Interestingly, we found that other behaviours besides digging were involved in the tool-assisted excavation of underground food: probing, perforating, pounding, shovelling and enlarging. As such, the excavation of artificially buried food (and presumably the excavation of USOs) does not involve a single tool behaviour but rather a repertoire. This would suggest that USO excavation by wild

Behaviour	Description
Probe	A chimpanzee holds one end of a tool and places the other end in a hole without using his/her body weight (generally while holding the tool with a precision grip but not necessarily). The hole can be open, completely or partially excavated. The tool is then withdrawn and the inserted end may or may not be visually and olfactorily inspected.
Perforate	A chimpanzee inserts a tool into the ground and applies force pushing the end of the tool into the ground with both hands or a hand and a foot, or one or both feet. Power grip is generally (but not necessarily) used if one of the hands holds the midsection of the tool. The tool is then retrieved and the end that went into the ground may or may not be visually and olfactorily inspected.
Pound	A chimpanzee holds a tool with one or both hands and with powerful back and forth movements of the tool, hits the ground repeatedly.
Shovel	A chimpanzee holds the midsection of the tool with one hand and with the other hand, or the opposite leg, holds the upper end of the tool. Then she/he inserts the lower end of the tool into the ground and forces it in until about half of the tool had penetrated. The chimpanzee then withdraws the tool outward, which results in the removed materials deposited outside of the excavated area.
Enlarge	A chimpanzee inserts a tool into an open hole and with sweeping, circular motions of the tool widens the opening. The tool stays in contact with the ground while rotating.
Dig	A chimpanzee holds a tool with both or one hand and inserts it into the ground at approximately arm length. Then, while pressing the tool in the ground, moves it powerfully inward towards him/herself – once or repeatedly.

(Source: Motes-Rodrigo et al 2019 table S2)

Table 3.2 - Descriptions of tool-use behaviours.

chimpanzees may be similar in complexity to other underground food source extractive tasks such as foraging for underground honey bee nests or termites. In the context of underground food excavation, the chimpanzees in our study selected tools for the task, reused some tools more frequently than others and transported tools. These behaviours have already been reported for chimpanzees in other contexts, considered complex, such as foraging for termites, honey and nut kernels" (pp18-19).



(OH1 = open hole condition in Experiment 1; LS1 = loose soil condition in Experiment 1; CC1 = compacted clay condition in Experiment 1; CS2 = compacted soil condition in Experiment 2)

(Source: Motes-Rodrigo et al 2019 figure 4)

Figure 3.6 - Proportion of each excavating behaviour in four conditions.

3.11. APPENDIX 3B - RECOGNITION

Suarez et al (2020) began: "Nearly every biological interaction requires some kind of recognition... Recognition systems, therefore, play critical roles in discriminating among beneficial and detrimental actors in diverse ecological and evolutionary contexts, including self, species, mates, kin, predator–prey and host–parasite interactions, and even habitat selection. Evolution should select for stringent recognition when mistakes are costly. Yet, both acceptance errors (eg: accepting a parasitic cuckoo's mimetic egg) and rejection errors (eliminating your own egg instead of the parasite's), which may severely reduce or altogether eliminate fitness of the erring discriminator, are common in many recognition systems" (p1).

In a classic paper, Reeve (1989) introduced the "conspecific acceptance threshold theory" [18], which involves an acceptance threshold under which there is acceptance, but above it rejection. The threshold can shift depending on the context (Suarez et al 2020).

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[18] This is an example of a signal detection theory (Suarez et al 2020).

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4. HONEST SIGNALS AND COMMUNICATION

4.1. HONEST SIGNALS

"Honest signalling" can be seen, for instance, in the size of the body of the caller accurately reflected in acoustic features of vocalisation (eg: louder call with larger body size) [19]. "Dishonest signalling" is where evolutionary adaptations of the vocal system, in this example, can exaggerate the impression of body size.

But within a species runaway selection is constrained by physical limitations (acoustic allometry)(Garcia and Ravignani 2020). In other words, smaller individuals, say, cannot keep evolving anatomical adaptations to sound bigger.

Two acoustic features are important in mammals - "fundamental frequency"("the rate of vibration of vocal folds in the mammalian larynx, ie: the sound source"), and "formant frequencies" ("specific resonances reflecting the geometry of the mammalian vocal tract, ie: the filter") (Garcia and Ravignani 2020) [20].

"Vocal production learning" (VPL) is the ability to modify existing vocalisations to produce new sounds, or to copy sounds that do not belong to the individual's vocal repertoire (Garcia and Ravignani 2020) (appendix 4A). Garcia and Ravignani (2020) argued that VPL could be a "cheating" strategy to overcome the limitations of acoustic allometry among mammals. In other words, "some species might have evolved the capacity for volitional vocal modulation via sexual selection for 'dishonest' signalling" (Garcia and Ravignani 2020 p1).

For example, among Southern elephant seals,

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[19] For example, among funnel-web building spiders, web vibration is a honest signal of body weight to opponents (Riehardt 1978).

[20] The formants are reliable cues to the caller's body size in adult American alligators (Alligator mississippiensis). Reber et al (2017) studied the formant frequencies in the bellow of 43 adults (thirteen female and 29 male) at a zoological park in Florida, USA, in 2013. Measurements were made of the body size of the individuals, and the bellows were recorded.

unsuccessfully breeding males have been observed to copy call types of successfully breeding individuals (Sanvito et al 2007; appendix 4B).

4.2. PURSUIT-DETERRENT SIGNALLING

Alarm calls signal danger and encourage anti-predator behaviours in conspecifics. Adams and Kitchen (2018) highlighted an "intriguing paradox" - "If alarm calls function solely in intra-specific communication, then signallers should produce as few calls as possible to allow conspecifics to detect the signal while still remaining inconspicuous to the predator... But, how do we account for group-living species that exhibit conspicuous behaviours in the presence of predators?" (p141). Vocalisations continue long after all members of the group are aware of the presence of a predator, and, sometimes, alarm calls are made in the absence of conspecifics.

One answer is that the alarm calls are also directed at the predator - ie: "pursuit-deterrent signalling". This is "a prey animal signalling that it has detected the predator, which causes the predator to give up its approach towards prey as a result of this information alone" (Caro 1995 quoted in Adams and Kitchen 2018). This is even more important in the case of ambush predators that rely on the element of surprise [21].

Experiments on this subject have tended to be in captive situations, and thus lack ecological validity (Adams and Kitchen 2018).

However, leopards have been reported in the wild to move away after hearing monkey alarm calls (eg: radio-collared leopards in the Tai Forest, Ivory Coast; Zuberbuhler et al 1999).

Adams and Kitchen (2018) made use of wild radio-collared ocelots (Leopardus pardalis) in Peru in 2014-15 in their study with the playback of alarm calls of two prey species of monkeys - titi monkey (Callicebus toppini) and saki monkey (Pithecia rylandsi). Ten alarm calls of each monkey species were used, and ten non-predator calls each (controls). The geographical location of four ocelots were measured at 15-minutes before and fifteen and thirty minutes after the playbacks.

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[21] Ambush predators use two main strategies :i) "Sit-and-wait" - remaining motionless for long periods waiting for unsuspecting prey to pass by.
ii) "Opportunistic hunting" - "quietly looking for prey while roaming through their habitat" (Adams and Kitchen 2018 p146).

Both strategies depend on not being detected, so it "is not surprising that once their presence has been detected, ambush predators would benefit by departing from an area for a new location where they might remain unnoticed" (Adams and Kitchen 2018 p146).

"Whereas ocelots remained hidden in the majority of control trials (11 of 19 trials, 58%), they moved away from the sound source in the majority of alarm trials (12 of 19 trials, 63%)" (Adams and Kitchen 2018 p144). This was fifteen minutes after playback. At thirty minutes, the ocelots continued to move away from the sound source in the alarm call condition. This showed that the ocelots could distinguish the different calls of the two species of monkeys. The findings also support the alarm calls as "pursuit-deterrence signalling".

This study had a small sample size. There was also an issue about the ecological validity of the experiment. Adams and Kitchen (2018) explained: "While cats remained in hiding after hearing loud calls not associated with predators in the majority of our control experiments, they actually moved towards similar sounds coming from real and presumably unaware monkeys (ie: those that were travelling, foraging and producing affiliative calls) during natural encounters. Although speculative, the difference in their behaviour may indicate that ocelots rely on additional visual and auditory cues when making decisions about pursuing prey" (p146).

Studies with other animals include (Adams and Kitchen 2018):

- African antelopes producing loud, repetitive alarm duets if a predator approached closer than 100 metres (Tilson and Norton 1981).

- Timber rattlesnakes move away when confronted by rodents making visual displays (Clark 2005).

4.3. LOUD CALLING BIRDS

The male white bellbird (Procnias albus) has "what are probably the loudest of all bird calls" (Snow 1982 quoted in Podos and Cohn-Haft 2019).

When observed in the Brazilian Amazon, these birds sing loudly in the presence of a female in close proximity. This could suggest that the loudness of the song is under pressure from sexual selection.

Podos and Cohn-Haft (2019) measured the sound levels at around 110-115 dB [22], and similarly in the screaming piha (Lipaugus vociferans) [23]. The researchers commented: "The extreme nature of the vocal display performances

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[22] As loud as a pneumatic road drill (Grossman 2019).

[23] Bitterns are thought to be the loudest bird in Britain - 101 dB (the equivalent to an outboard motor), and nightingales in urban areas have reached 95 dB (Grossman 2019).

documented here imply that pihas and especially bellbirds sing at or near their maximal performance capacities" (Podos and Cohn-Haft 2019 pR1069).

This leads to a trade-off - "as birds up-regulate respiratory air flow to elevate song amplitude, they deplete their respiratory tidal volumes more quickly, leading to shorter-duration songs. This constraint could presumably limit further evolutionary elaboration in amplitude even in the face of strong and persistent sexual selection" (Podos and Cohn-Haft 2019 pR1069).

The researchers reflected on their observations: "It is curious that one of the world's loudest birds sings only its highest-amplitude song type in such close-range communication. Animals normally reserve loud calls for communication over long distances, and some species are known to vocalise more softly when receivers are nearby. It is also unclear why female white bellbirds willingly stay so close to males as they sing" (Podos and Cohn-Haft 2019 pR1069).

4.4. ORANG-UTANS AND CONTAGIOUS SCRATCHING

"Behavioural contagion" is "a phenomenon in which a behaviour is automatically triggered by the perception of a similar behaviour in others" (Lameris et al 2020 p1) (eg: yawning). Lameris et al (2020) explained: "While spontaneous yawning (ie: non-social yawning) is widespread across vertebrates and may function in promoting cortical arousal..., and/or changing emotional states through decreasing brain temperature..., contagious yawning is restricted to fewer species in which this trait may have evolved independently" (p2).

Such behavioural contagion is stronger between kin, and is assumed to facilitate group cohesion (Lameris et al 2020).

Contagious yawning has been studied in several primate species (eg: chimpanzees, bonobos), though not all research agrees (Lameris et al 2020).

Scratching is another contagious behaviour, and it is associated with arousal and stress. "For example, increased scratch rates have been reported during aggressive interactions..., post-conflict interactions without reconciliation..., dominance-related interactions..., and predation attempts... Concurrently, scratching behaviour is reduced after play bouts during affiliative interactions..., and after reconciliation following aggressive interactions" (Lameris et al 2020 p2).

Lameris et al (2020) studied contagious yawning and scratching among nine captive adult Bornean orang-utans (Pongo pygmaeus) in the Netherlands. Contagious was defined as the same behaviour by another individual within three minutes of the original expressor.

There were insufficient data on yawning over the three months of observations, but there was evidence of contagious scratching. "Furthermore, when the relationship quality between the expresser and observer was low, and the observer had seen the triggering scratch, scratch contagion was more likely to occur during tense situations" (Lameris et al 2020 p5). It was possible that "emotional contagion" was happening, argued Lameris et al (2020).

The researchers also talked on scratching as a form of communication. They stated: "Some other studies have reported on the potential signalling function of scratching. For instance, recent studies show that scratching can be used as a signal to co-ordinate joint travel, for example, between a mother and infant..., and may be used to initiate grooming... Another possible communicative function of scratching is to signal social distress, which in turn reduces the likelihood of receiving aggression... In our study, it is possible that orang-utans use scratching in others as a marker of arousal and that the automatic contagion of such information from weakly bonded individuals during tension has an adaptive value" (Lameris et al 2020 p6).

4.5. LEMURS AND ODOURS

Among primates, strepsirrhines (eg: ring-tailed lemur) have well-developed olfactory communication. Males have scent glands on their wrists (antebrachial scent gland) and shoulders (brachial scent gland), which they use to advertise their rank status, reproductive status, and to demarcate territory (Shirasu et al 2020).

During the breeding season, males "rub their antebrachial and brachial scent glands on their own tails and then wave their tails to spread the glandular volatiles that threaten other males. With these behaviours, the male lemurs display their dominance status to potential rivals within the small multi-male-multi-female groups" (Shirasu et al 2020 p2131).

The use of odours in male-female communication is less well-known. Shirasu et al (2020) rectified this failing with their recent study of ring-tailed lemurs at the Japan Monkey Centre.

The duration of female sniffing of male scent marks was measured in and out of the breeding season. "Females sniffed male scent marks during the breeding season significantly longer than during the non-breeding season...[median 5 vs 2 seconds]... This result indicates that female lemurs are more attracted to male scent gland secretion during the breeding season" (Shirasu et al 2020 p2133). The researchers were able to chemically analyse the secretions, and identified three (with a "fruity and floral scent"). Females sniffed longer on these three than other chemicals when presented on cotton pads.

4.6. ACOUSTIC CRYPSIS

While adults of a species may be relatively safe from predators, their cubs or calves can be highly vulnerable. This is the case with the southern right whale (Eubalaena australis) and killer whale (orca) predation. For example, mother-calf pairs reside in shallow water as a refuge from predators (Nielsen et al 2019).

These animals, like many baleen whale species, are slow reproducers (ie: many years between offspring), and nursing a calf is a large energy investment. The use of acoustic communication between the mother and calf is important, particularly in low-visibility waters, but the orca can eavesdrop (Nielsen et al 2019).

How to balance the risks and benefits of acoustic communication? Nielsen et al (2019) found evidence of "acoustic crypsis" as a strategy in their study of southern right whale mother-calf pairs in their breeding ground off Western Australia. Recordings were made in August 2016 and 2017.

Nine lactating tagged females were recorded for a total of over sixty hours. Maternal calls were most frequent when diving, "indicating that these signals are used as cohesion calls that function to maintain contact when the whales are moving or becoming separated" (Nielsen et al 2019 p5). Otherwise, the calls were infrequent as a rule (eg: less than ten calls per hour).

The acoustic crypsis was seen in the "camouflaging" of low amplitude calls with elevated ambient noise (eg: waves on the shore). It was calculated that the calls would not be detectable above 200 metres away (Nielsen et al 2019).

4.7. DECOY NESTS

Female sea turtles lay large clutches of eggs (eg: 50-100) in nest cavities in sand beaches, and leave (ie: no parental care). "There is variation in their description and categorisation within and between species, but they broadly follow these steps: emergence from the sea and movement up the beach, selection of nesting site, preparation of nest site (body pitting), excavation of egg chamber, oviposition (egg laying), refilling of the egg chamber, scattering or throwing sand around the nest site (usually referred to as the 'camouflaging' or 'disguising' stage) and then return to the sea" (Burns et al 2020 p2).

The nests are vulnerable to predators during the egg incubation period.

Burns et al (2016) reported that leatherback turtles (Dermochelys coriacea) spend a long time on the throwing of sand phase, and it is "potentially the most metabolically expensive" (Burns et al 2020 p2). The females also "move considerable distances away from their nests, stopping periodically to scatter sand while tracing a convoluted route that rarely if ever impinges upon the nest itself" (Burns et al 2020 p2). This was termed "sand-scattering" (Burns et al 2016).

Two main hypotheses have been proposed for the behaviour (Burns et al 2020):

i) To "camouflage" or "disguise" the nest site from predators.

ii) To "(re-)establish the beach environment around the nest to optimise temperature and moisture conditions for egg development" (Burns et al 2020 p7).

Burns et al (2020) compared sand-scattering behaviour in leatherback turtles with the hawksbill turtle (Eretmochelys imbricata). They were both observed at different sites in Trinidad and Tobago between 2014 and 2019.

Both species showed sand-scattering behaviour. The number of stops to scatter sand varied from 1 to 14 for hawkbills, and 5 to 24 among leatherbacks, and the distances between scattering stops ("stations") varied from 6 to 147 cm, and 22 to 318 cm respectively.

Burns et al (2020) rejected both hypotheses above for the behaviour because the sand-scattering disturbed sand more not less. These researchers preferred a "decoy" explanation. They stated that "the nest-like decoy disturbances in the sand... while making the general nesting area more obvious, may confuse predators as to the exact position of a nest and increase the search and excavation effort required to find it. Increased search and excavation costs have been shown to alter nest predator foraging behaviour and predation risk" (Burns et al 2020 p7). This would fit with the time and energy expended by the females on this phase of egg-laying.

4.8. APPENDIX 4A - BATS AND VPL

Lattenkamp et al (2020) provided evidence of VPL in the pale spear-nosed bat (Phyllostomus discolor) in an experiment with artificial calls. Six males were trained to mimic social calls, which triggered a feeder to open. Then the playback calls were downward pitch-shifted by four semi-tones. The bats showed that they could voluntarily change their pitch to mimic what they heard. There were individual differences between the bats.

4.9. APPENDIX 4B - SANVITO ET AL (2007)

The Southern elephant seal (Mirounga leonina) has a mating system based on harems ("female defence polygyny"). This means that the "strongest" males only mate, and they defend this right ("resource-holding") in inter-male competition, which includes agonistic vocalisations.

Sanvito et al (2007) studied the copying of dominant male vocalisations by younger males using data from eight breeding seasons (1995-2002) at Sea Lion Island, Falkland Islands (table 4.1). Audio recordings were made of male aggressive vocalisations, and the "bouts" were categorised into six types based on fifteen variables including "syllables" and "syllable parts".

- Observations by 2-4 observers for two-hour periods randomly across the day, tidal phases, breeding beaches, and harms.
- A total of 15 694 agonistic interactions between males observed.
- All males individually marked with tags and dye marks.
- "All-occurrences sampling": all agonistic interactions and copulations recorded during the observation period.
- 103 hours of male vocalisations recorded.

Table 4.1 - Details of the data collection.

One-fifth of males were harem-holders, and they were involved in two-thirds of the agonistic interactions, usually initiating and the other male ("peripherals") responding. Half of these interactions were settled by vocalisations alone, while optical displays (eg: of size), chasing, and fighting were also used.

Of 21 young males recorded, 57% adopted a "vocalisation type" of the harem-holder that they would have heard growing up. This was not genetic because the imitators were not genetically related to the harem-holder, where this information was known. Sanvito et al (2007) concluded that "vocal learning by imitation of the most successful breeding males (ie: those holding the largest harems) is the most reasonable and parsimonious explanation for our observations" (p143).

The researchers noted that young males on shore during the breeding season "have little chance of reproducing but pay a high cost for attendance because they fast while on land and lose substantial body mass...

Fasting costs may be offset by gains in social experience, which improves competitive abilities in subsequent years" (Sanvito et al 2007 p144). They speculated: "At Sea Lion Island, vocal imitation by young individuals of reproductively successful males may be an important component of the development of social competence. The breeding ground is the only place where young elephant seals can learn and practise the vocalisations that are so important in later social life" (Sanvito et al 2007 p144).

Because of the dominance hierarchy of these seals, there is strong selection pressures on the behaviour that establishes and maintains dominance, like vocalisations. "Vocalisations seem to transmit information about the resource-holding potential of the emitter... Therefore copying the syllable structure of successful males may be a form of cheating... [But] other acoustic features (frequency and intensity) seem to encode information about phenotype..., making the spread of truly dishonest signals unlikely" (Sanvito et al 2007 p144).

This study was longitudinal, though causation of relationships could not be established.

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5. MULTIPLE MATING

5.1. LEK SPECIES

"Multiple mating" is defined as "a female copulating with more than one male during a single reproductive event" (Kempenaers 2020 p1138) (appendix 5A).

Ideally, a female can increase the probability of survival of her offspring by choosing a male with high quality genes and resources. But one individual may not have both of these, so a female gets the "best of both worlds" by pairing with the owner of resources, while also mating with the owner of good genes (known as extra-pair copulations; EPCs) (Kempenaers 2020).

Among some species, males provide no resources and there is no pair bond/male parental care, so sperm is all they give the female. These species use leks - sites where males temporarily congregate during the breeding season to advertise their quality, and females can compare what is available and choose. It is expected that females will copulate with the preferred male only, and so multiple mating is not necessary in lekking species.

"However, not only does it occur, it even seems relatively common. Multiple paternity has been detected in every lekking species studied (N = 8), varying in frequency between 3.4% and 50% of broods (Hess et al 2012). Multiple mating has also been reported in the lekking peacock Pavo cristatus: 50% of marked peahens were observed to mate more than once and of those 78% copulated with 2–5 different males (Petrie et al 1992)" (Kempenaers 2020 p1139).

Another example is the lance-tailed manakin (Chiroxiphia lanceolata). Rivers and DuVal (2020) found that 7-22% of 465 sampled clutches of two eggs had different fathers. Data were collected in Panama between 2000 and 2013 from 216 females.

The lance-tailed manakin has a spread-out lek (called an "exploded lek"), and displays are made by two unrelated males (referred to as the alpha, who mates if successful, and the beta who is less likely to mate) (Kempenaers 2020).

One explanation for the findings is that "females prefer males with high social status or with more experience and that they will therefore be less inclined to copulate with another male if they have first mated with such a preferred male. Multiple paternity would then occur if females made a non-optimal choice at first" (Kempenaers 2020 p1139). This could be called the "active female choice hypothesis" (Kempenaers 2020).

The mating dance is complex and improves with experience. But less experienced males might get it right sometimes, and this leads the female to choose them. Kempenaers (2020) suggested a scenario where "females evaluate the same male repeatedly and may realise that they copulated with one that was not such a good dancer after all and then decide to copulate with another male" (p1140).

Another possibility is that females copulate with multiple males as insurance against infertile sperm ("fertilisation assurance"), or sperm competition takes place after mating (ie: the more competitive sperm inseminate the egg) ("genetic bet-hedging") (Rivers and DuVal 2020) (appendix 5B). Rivers and DuVal (2020) found little evidence for these ideas.

Kempenaers (2020) proposed the "male endurance hypothesis". Females visit the lek site before mating, assess the options, and later return to copulate with her choice. But recall may be based on the site of the dancer, and usually the experienced alpha male, who knows when the female is likely to return, is there, but "in the rare cases he happens to be away, the beta or a less-experienced alpha displaying nearby will have an opportunity to fertilise an egg" (Kempenaers 2020 p1140).

Rivers and DuVal (2020) could not fully explain the multiple matings in their study. They stated: "When females are unconstrained in their choice of mate and are free to assess males prior to copulation, variation in the frequency of multiple mating may result from a multitude of factors. In lance-tailed manakins, multiple paternity by females is not the result of consistent individual differences in the tendency to mate with multiple males and is also not the result of individual female experience, but rather seems to be driven by female encounters with males of different experience levels. Our results suggest that multiple mating by females may be driven by breeding male experience but does not have obvious benefits for females" (Rivers and DuVal 2020 p1150).

5.2. APPENDIX 5A - THEORIES FOR MULTIPLE MATINGS

i) Experience level - Inexperienced females make multiple matings because they are not good at assessing male quality (eg: black grouse; Kokko et al 1999).

ii) Sneaky copulations - Lower

status/quality/experienced males are able to sneak copulations, and females realise and subsequently mate with higher status/quality/experienced males.

iii) Individual differences - Some females make multiple matings, others do not (eg: boldness and great tits; Patrick et al 2012).

iv) Fertilisation assurance - Just in case the single mate is infertile, and to avoid wasted investment in an egg that did not develop.

v) Genetic bet-hedging - To increase the genetic diversity of her offspring (eg: sierra dome spider; Watson 1991).

5.3. APPENDIX 5B - POST-COPULATION EFFECTS

After copulation, female fruit flies (Drosophila melanogaster) reject subsequent males, as well as show changes in sleep, activity, and diet. "All these changes are mediated by a sperm-bound peptide, the sex peptide (SP), which is transferred into the female's reproductive tract during mating" (Scheunemann et al 2019 p1).

Scheunemann et al (2019) also discovered an increase in long-term memory (LTM) for aversive smells after mating. The researchers compared the 24-hour memory of virgin females, mated females, and females who mated with a "mutant" male (ie: no SP) by pairing a particular smell with a mild electric shock. A tube with a different smell at each end was used for training and testing.

SP was seen as responsible for improved memory as virgin females injected with a synthetic version had a better memory.

Scheunemann et al (2019) asked and answered an obvious question: "Why does aversive LTM increase after mating, while it is inhibited in virgin females? Increased aversive LTM after mating could elevate the survival chances of females during egg laying and favour the choice of secure egg deposition sites" (p8).

5.3.1. SEX SELECTION

It has recently been found that certain chemicals slow down sperm that carry the X chromosome. Use of that knowledge could be applied to "choose" the sex of a fertilised egg (which usually means a preference for a boy) (Le Page 2019).

Umehara et al (2019) found that sperm carrying the X chromosome (which leads to female offspring) has certain genes active that are not so in sperm carrying the Y chromosome (which leads to male offspring). Some of these genes code for proteins that stick out from the sperm cell's surface, so chemicals that bind to these proteins can slow the sperm down.

Working with mice, Umehara et al (2019) found that slowing down sperm led to 90% of pups being male. How long before a gel, say, is produced to apply to human vagina prior to sex? "There is likely to be an appetite for such products, especially in countries where sex ratios have already been distorted in favour of boys" (Le Page 2019 p6).

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6. CARE AND SOCIALITY

6.1. BEARS AND MATERNAL CARE

"Parental care and its duration can limit reproductive opportunities for both sexes, leading to a sexual conflict over the duration of those care, even in species where care is provided by one sex only" (Van de Walle et al 2019 p2). In the case of mammals, the majority of whom have maternal only care, lactation suppresses oestrus. This is a cost to both sexes, but maternal care can offer compensatory benefits (eg: increased survival chances of offspring).

The weaning of offspring (ie: stopping maternal milk feeding) seems to be linked to their body mass (eg: prolonged care for smaller offspring), and mother-offspring separation (or offspring dispersal) can depend on environmental conditions. For example, female leopards have been found to prolong care of their cubs if there is prey scarcity (Van de Walle et al 2019).

Males may respond to the length of maternal care with sexually selected infanticide (SSI), "where a male kills unrelated offspring to then mate with the victimised female" (Van de Walle et al 2019 p2). Less extreme alternatives include forcing early weaning or dispersal, or abortion (Van de Walle et al 2019).

A counter-strategy for females in this sexual conflict is to avoid males by spatial segregation. "In brown bears, female with cubs-of-the-year can alter their habitat and daybed selection patterns... to avoid dominant adult males during the spring and early summer, ie: the period of high risk for sexually selected infanticide... In some populations, females even have been reported to use human presence as a shelter against males" (Van de Walle et al 2019 p2).

Van de Walle et al (2019) focused on this latter strategy among Scandinavian brown bears (Ursus arctos), who have a period of maternal care of 1.5 to 2.5 years. Observations were made in south-central Sweden, which has a sparse human population [24]. Most of the bears had been given a GPS collar. Females were divided into those providing maternal care for 1.5 years ("short-care females"; n = 11) and for 2.5 years ("long-care females"; n = 8). Data were available for 2004 to 2016.

Van de Walle et al (2019) summed up their findings: "Females that provided short maternal care selected for habitats similar to those selected by males. In contrast, we found significant differences in habitat selection patterns between males and females that kept their yearlings for an additional year. The most striking difference was that long-care females strongly selected for human habitations, whereas males avoided human habitations. We hypothesise that by reducing the probability of encounters with males, spatial segregation from males through spatial association of females with humans may allow for continued maternal care in brown bears" (p6).

The "short-care females" may have intentionally chosen areas where males would be encountered because they wanted to encourage offspring dispersal and to mate again. On the other hand, the choice of habitat close to males may have been unintentional. The risk of SSI has been estimated at 3-16% of yearlings in the study area (Van de Walle et al 2019).

To avoid SSI, mothers may chase their cubs away. "In several primate species where males pose a threat to offspring, the arrival of a new male in a group has been associated with abrupt weaning and/or maternal rejection, irrespective of the age of the infant and even in the absence of aggressions... For instance, in captive vervet monkeys (Cercopithecus aethiops sabaeu), females placed with a new male reject their infant more frequently near the expected weaning age, even without being harassed, compared with when placed with a resident male (Fairbanks and McGuire 1987)" (Van de Walle et al 2019 p7).

For the "long-care females", did they choose to be near humans (and so away from males) to allow for long-term care, or did being spatially segregated lead to the opportunity to care for another year? Van de Walle et al (2019) could say for definite.

Living near to humans did not necessarily provide the best food sources, and also had the risk of disturbance and hunting. The "despotic distribution hypothesis" (Fretwell and Lucas 1969) suggested that "the most vulnerable individuals may be forced into sub-optimal habitats" (Van de Walle et al 2019 p9).

Altogether, for "females with offspring, the risk of living in close proximity to humans appears to be

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[24] Distance to human footprint (based on roads and habitation) was calculated by drawing a random sample of locations within the home range of the bear.

outweighed by its fitness benefits. Indeed, cub survival is improved when Scandinavian brown bear females with cubs-of-the-year employ such a safety-search tactic and use humans habitations as shields against males (Steyaert et al 2016)" (Van de Walle et al 2019 p9).

6.2. VAMPIRE BATS AND SICK INDIVIDUALS

Sickness can alter an animal's behaviour. On the one hand, pathogens may manipulate the individual to engage in more social interactions in order to favour their transmission. The alternative is "sickness behaviour" ("lethargy") where the individual becomes less active and with lower social encounters. In social animals, healthy individuals may avoid sick ones to reduce pathogen transmission (Stockmaier et al 2020).

The behaviour of the common vampire bat (Desmodus rotundus) has been studied in terms of the social group's response to sick individuals. Stockmaier et al (2018), for example, tested a small number of bats in a controlled environment. Certain individuals were injected with an immunostimulant (lipopolysaccharide; LPS) to produce the transient symptoms of a bacterial infection. Two social behaviours were observed - allogrooming (licking another's body) and food sharing (regurgitation of blood).

Stockmaier et al (2020) replicated this study with a larger captive colony (36 bats) in Panama. Individual bats were removed from the colony briefly, injected with LPS or saline (control), and replaced. The subsequent behaviour of the colony was video-recorded and scored.

LPS-injected bats groomed others less and were groomed by fewer others than controls, but food sharing, which is a rare behaviour only for bats in dire need, did not vary between conditions. "Mothers did not groom their offspring less when either the mother or their offspring were immune-challenged" (Stockmaier et al 2020 p1392).

Stockmaier et al (2020) summed up: "In general, our results indicate that sick conspecifics were not actively avoided, nor did they isolate themselves. Instead, our observations were most consistent with the simplest explanation that reduced social interactions resulted from LPS-injected bats being lethargic" (p1392).

The failure to avoid sick individuals would suggest that the overall benefits of social interactions outweigh the benefits of avoidance or the cost of continued interaction. This is particularly seen in the observation that maternal grooming was unchanged. So, "it is likely that reducing maternal care is more costly to fitness than the physiological risks posed interacting with an infected bat" (Stockmaier et al 2020 p1392).

Stockmaier, Bolnick et al (2020) concentrated on the contact calls of sick individuals, and showed that LPS-injected isolated vampire bats produced fewer. Eighteen female bats participated in both conditions (LPS and saline injection) in a random order.

The average contact calling rate was 66 per hour in the control condition compared to sixteen in the LPS condition.

LPS-injection experiments have found reduced vocal communication in other species, including house mice, and selected birds (Stockmaier, Bolnick et al 2020).

Calling is energetically demanding, so sick individuals can reduce metabolic costs by reducing it. This fits with the "lethargy" explanation of sick individuals. Stockmaier et al (2018) noted that LPS-injected bats spent less time awake, and moving.

It is possible that sick individuals could increase their calling in order to gain benefits from others (eg: food), and this would also be an advantage to the pathogen (eg: chytrid-fungus infected Japanese tree frogs increase mating call; An and Waldman 2016).

Both studies with LPS only mimicked bacterial infection, whereas pathogens have specific effects. For example, bats infected with rabies become more aggressive (Stockmaier et al 2020).

6.3. CATS AND ATTACHMENT

Between domestic dogs and cats, the former are viewed as having developed human-like socio-cognitive abilities. But this underestimates cats (Felis silvestris catus), argued Vitale et al (2019).

Their research showed attachment bonds between cats and their owners, which had previously been noted for dogs only. The Secure Base Test (SBT) is an adapted version of the "strange situation" test developed to measure attachment between human infants and their caregivers. In the SBT there are a series of two-minute episodes in a novel room - (i) cat and owner together; (ii) cat alone; (iii) reunion with owner. The behaviour of the cat in each episode is scored to give an attachment type (secure, or three types of insecure attachment).

Vitale et al (2019) outlined the basic expected patterns of behaviour: "Upon the caregiver's return from a brief absence, individuals with secure attachment display a reduced stress response and contact-exploration balance with the caretaker (the Secure Base Effect), whereas individuals with an insecure attachment remain stressed and engage in behaviours such as excessive proximity-seeking (ambivalent attachment), avoidance behaviour (avoidant attachment), or approach/avoidance conflict (disorganised attachment)" (pR864).

Seventy kittens aged 3-8 months old were tested in the USA - of which two-thirds were categorised as securely attached, just under 30% as ambivalent attachment, and the remainder as avoidant or disorganised attachment. Similar percentages were found among 38 adult cats tested in the SBT by Vitale et al (2019).

Vitale et al (2019) concluded: "The current data support the hypothesis that cats show a similar capacity for the formation of secure and insecure attachments towards human caregivers previously demonstrated in children (65% secure, 35% insecure) and dogs (58% secure, 42% insecure) with the majority of individuals in these populations securely attached to their caregiver" (pR865).

6.4. ORPHAN CHIMPANZEES

In species where the offspring depend on maternal care after birth, the young are vulnerable if the mother dies. "Orphans may survive, however, if they find another individual who provides care similar to a mother" (Reddy and Mitani 2019 p389). "Maternal-like caregiving" or "adoption" of orphans has been observed in various mammals including red squirrels, bottlenose dolphins, and various monkeys. Older maternal siblings are the most common adopter (Reddy and Mitani 2019).

Reddy and Mitani (2019) studied the situation in chimpanzees after a disease outbreak in Kibale National Park, Uganda, led to thirteen individuals losing their mothers in 2016-17. Around 200 chimpanzees were part of a long-term observational study since 1995.

The social behaviour of orphaned males with maternal siblings, and males with living mothers were observed for three hours per individual. There was also data available on the orphans before the mother died.

"After losing their mothers, recently orphaned chimpanzees intensified their social interactions with at least one of their maternal siblings if they had one" (Reddy and Mitani 2019 p397). Orphaned males spent more time with maternal siblings than when the mothers were alive (mean 84% vs 58% of time), and they stayed in closer proximity. Also there was increased grooming (mean 3.03 minutes per hour vs 0.13 before death), reassurance (eg: hand-holding; embracing), and vigilance (eg: looking back for the other individual and stopping while travelling) by orphans.

Reddy and Mitani (2019) explained further:
"Virtually all social behaviour between orphaned siblings was initiated by younger siblings, indicating the active role they played in the relationships. Younger siblings

typically started grooming and groomed their older sibling more than they received grooming from them though this was not the case for all pairs. They were almost always the ones to seek reassurance, approach, and maintain spatial proximity, and follow their older siblings during travel. Still, it seemed important to older siblings that this spatial proximity was maintained, especially during travel. While their younger siblings approached and followed, older siblings often waited for them to catch up and finish feeding. Older siblings also looked for their younger brothers and sisters before travelling, sometimes backtracking or standing bipedally to extend their view. This leaving and waiting pattern mirrors that shown by mothers to their dependent offspring; mothers typically leave their juvenile offspring when they begin to travel, but wait for them to follow" (p398).

The researchers noted in summary: "These findings suggest that siblings provide each other support after maternal loss. Further research is needed to determine whether this support buffers grief and trauma in the immediate aftermath of maternal loss and whether sibling support decreases the probability that orphans will suffer long-term consequences of losing a mother if they survive" (Reddy and Mitani 2019 p389).

6.5. COWS AND ALLOGROOMING

Allogrooming (or social grooming) is important in socially stable groups, as in cattle. "Inter-individual bonds and preferential relationships are mainly established, maintained, and reinforced through allogrooming. This behaviour also enhances group cohesion and maintains social stability, reduces social tension and has calming effects" (de Fresion et al 2020 p2).

de Fresion et al (2020) observed cows at a dairy farm in Chile, and recorded the allogrooming (defined as "a cow repeatedly using her tongue to lick any part of the body of another cow, except the ano-genital area"; p3) over six weeks. Five observers at a time conducted 30-minute observation periods, which allowed for inter-observer reliability. The social rank of an animal was determined by headbutts towards others (and converted into a dominance index; DI) [25].

The cows were then grouped into three for convenience based on DI - low-, medium-, and high-ranked. In total 38 cows were observed in 1329 allogrooming events. The aim of the researchers was to establish the

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[25] The researchers noted that "there is still no consensus on the most appropriate method to determine social rank in dairy cows" (de Fresion et al 2020 p8).

social network of interactions.

"There was a substantial amount of variability in the intensity of performing but also receiving allogrooming, indicating individual differences among cows. Some cows were very active and central in the network, while others almost did not interact. Previous studies on social grooming in cattle found similar results, suggesting that specific individuals might be key players in the network structure" (de Fresion et al 2020 p7).

Reciprocal allogrooming was observed in about a quarter of cases (ie: a tendency to groom other cows who have previously groomed them).

High-ranked cows were licked by significantly less individuals than other cows. Previous research is divided about this finding (de Fresion et al 2020).

Older cows, who were more likely to be higher ranked, were more active groomers, which the researchers speculated was to "maintain herd stability and cohesiveness" (de Fresion et al 2020 p9).

There was also a "significant transitive triplets effect... In other terms, if a cow A groomed a cow B, and B groomed a cow C, then A was more likely to groom C subsequently ('the friend of my friend is also my friend' effect)" (de Fresion et al 2020 p9).

The researchers accepted that "allogrooming patterns are probably influenced by factors such as group composition, in relation to social rank and age distribution, and the resources available" (de Fresion et al 2020 p9).

6.6. OCTOPUS

California two-spot octopuses (Octopus bimaculoides) are an "anti-social" species in that individuals prefer to stay apart (or fight if together) (Nuwer 2018).

Edsinger and Dolen (2018) placed two adults in a tank with one of them in a mesh pot for safety, and the free swimming one moved as far away as possible [26]. Then the adults were given the drug MDMA, which increases serotonin and sociability in humans. The free swimming octopus spent more time close to the caged partner.

Technically, the three-chambered social approach task was used. This is a glass aquarium divided into three equally sized chambers. An octopus in a perforated plastic container is placed in one chamber (social chamber), and a novel object (eg: plastic toy) in a

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[26] But "somewhat surprisingly, both male and female subjects did exhibit social approach to a novel female conspecific" (Edsinger and Dolen 2018 p3139).

container in another chamber (object chamber), while the free-swimming octopus is placed in the centre chamber. The time spent in the object or social chamber during a 30-minute test session was used as the measure of sociability. Significantly more time was spent in the social chamber after MDMA than before administration.

6.7. MUTUALISM

Hematophagous flies (eg: deer and horse flies) feed on the blood of mammal hosts. They "inflict painful, irritating bites that can cause extreme physical discomfort..., create bleeding wounds and sores..., and facilitate the spread of bacterial... and viral... diseases" (Palmer et al 2019 p170). During the peak of the deer fly breeding season, this is little defence that deer have against attack.

The high volume of flies attracts their predators. Palmer et al (2019) recorded bats of unidentified species circling white-tailed deer in Minnesota who were under "fly attack".

Camera trap data over eight weeks of the summer of 2014 supported "a form of positive interaction appearing to benefit at least one, perhaps both participants, while harming neither" (Palmer et al 2019 p171) between deer and bat. This symbiotic relationship [27] benefits the deer in the removal of flies, and bats have plenty to eat with less foraging search time.

A similar behaviour has been documented with the bird, the oxpecker eating ticks of ungulates in the African savannas, and cleaner fishes removing parasites from larger reef fishes (Palmer et al 2019).

Palmer et al (2019) admitted that they could not "ascertain whether deer and bats are actively seeking each other out for this service nor assess whether either party gains demonstrable long-term fitness benefits from this association" (p171).

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7. HOME RANGE AND CO-EXISTENCE VERSUS MIGRATION

7.1. HOME RANGE

Home range formation is an example of animal space use, and it "occurs whenever animals restrict their movement to an area of the landscape far smaller than they could cover given their locomotive capabilities" (Ellison et al 2020 p2). The reasons for this behaviour include avoiding conflicts with conspecifics, or predators. Many home ranges have a "central point" (like a nest), and many animals advertise their territory through scent cues, say, or "ritualised aggression" (eg: vocalisations; domestic displays; fighting). But there are animals that have no "central point", and show no territorial behaviour (Ellison et al 2020).

One such example is the long-tailed tit (Aegithalos caudatus) (figure 7.1) outside the breeding season, who live in flocks of 5-25 individuals with slightly overlapping home ranges [28]. "They do not maintain a fixed roosting site, so have no clear localisation centre, and have rarely been observed to engage in territorial interactions" (Ellison et al 2020 p2).

Ellison et al (2020) found that avoidance of other flocks was a proxy for territoriality. Data were collected in a well-studied area of northern England from 2010 to 2013 and 2018-19. The approximate home range site for a flock was 0.15 km² of woodlands, and eight flocks were well observed.

Mathematical modelling of the observational data, Ellison et al (2020) explained, suggested that "flocks avoid places they remember interacting with other flocks in the past. These interactions could be visual or vocal, and therefore may take place at a distance... The memory capacity of small passerines is hard to test biologically

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[28] Ellison et al (2020) described the situation: "One or more fledged broods and their parents and helpers are usually the nucleus of a winter flock, which are then joined by failed breeders who may or may not be related to the brood(s)... Thus, the majority of flock members (60%–70%) are typically related ... to at least one other member of the same flock, although those relatives may be drawn from two or more families... In addition, members of one flock often have relatives in other flocks as a result of dispersal during the non-breeding season... Members of a flock forage together in the day and then sleep together in a communal roost, which often changes location between nights" (p3).

(Source: Slawek Staszczuk)

Figure 7.1 - Long-tailed tit.

as little is known about the cognitive abilities of small birds in general, regardless of species... However, the avoidance behaviour observed here would be very hard to explain without assuming some capacity for memory: to have an understanding of the spatial extent of the home range of a neighbouring flock (or even just the dividing boundary), birds would need to remember observations of past positions where they have detected the neighbouring flock, either through sight or sound. Without memory, birds would only be able to respond to the current location of a neighbouring flock, which is insufficient for explaining the observed spatial segregation" (p10).

The avoidance was also negatively associated with relatedness between flocks, and the size of the flocks, such that "smaller flocks were less likely to move to places where they had interacted with larger flocks in the past and larger flocks were less likely to avoid places where they had encountered smaller flocks, suggesting greater avoidance of larger flocks" (Ellison et al 2020 p10).

Ellison et al (2020) considered the possible explanations for the avoidance of other, particularly unrelated, flocks:

i) To avoid antagonistic social interactions - Napper and Hatchwell (2016) produced antagonistic interactions in playback experiments, so these birds can become aggressive.

ii) As an anti-predator tactic - ie: very large flocks could attract the attention of predators.

iii) Long-tailed tits are co-operative breeders which means that the breeding pair have helpers, usually kin, to raise the young. "Kin recognition is achieved through association using learned vocal cues... and helping decisions are also influenced by association during the non-breeding season... Therefore, there are substantial fitness benefits to be gained by maintaining contacts with relatives during the winter, and perhaps also by avoiding dilution of those associations by frequent interaction with non-kin in other flocks" (Ellison et al 2020 p11).

"The geographical range and abundance of species, however, can be highly variable: a species can be widespread but have low abundance throughout the range or only be found in a small geographic range but have high abundance" (Allen et al 2018 p90). The honey badger (Mellivora capensis) is an example of the former. They are solitary animals with large home ranges (eg: over 500 km^2 for adult males) in sub-Saharan Africa (and the Arabian and Indian peninsulas) (Allen et al 2018).

Honey badgers could be at risk from large carnivores, and Ramesh et al (2017) argued for an avoidance strategy. But Allen et al (2018) did not find this.

They reported a camera trap survey in the Serengeti National Park in Tanzania involving 224 camera traps between 2010 and 2013. The data suggested that honey badgers "seek out similar habitats and niches as larger carnivores" (Allen et al 2018 p92). One reason is that "honey badgers are notorious for their aggressive behaviour and high resource holding potential even when faced with much larger carnivores... Their aggressive threat display is often successful in preventing predation even against largest of carnivores, such as African lions, spotted hyenas, and leopards" (Allen et al 2018 p92).

Note that 29 honey badger camera trap captures were recorded out of 98 644 total trap nights.

7.2. INTERFERENCE COMPETITION

Top predators in an ecosystem killing, harassing, or stealing food from smaller predators is known as "interference competition" (Swanson et al 2016).

Smaller predators co-exist with the top predators by spatio-temporal avoidance - ie: avoiding certain areas, and/or times of the 24-hour period. "For example, foxes avoid habitats used by European lynx..., and coyotes concentrate primarily at boundaries between wolf-pack territories... These avoidance strategies can be costly: By restricting their activity to 'safe' areas or times of day in what is referred to as a 'landscape of fear' (Laundré et al 2001), sub-ordinate species can lose access to vital resources such as prey, water, or shelter" (Swanson et al 2016 p8535) [29].

Swanson et al (2016) used camera trap data (the same as Allen et al 2018) to understand the avoidance patterns among lions (top predator), spotted hyenas, and cheetahs in the Serengeti National Park. There was limited interference competition found. "In fact, hyenas and cheetahs were positively associated with lions except perhaps in areas with exceptionally high lion use; similarly, cheetahs showed no evidence of avoiding hyenas except in areas of extremely high hyena use. Fine-scale temporal analyses further indicated that hyenas and lions actively tracked each other, whereas cheetahs actively avoided lion-occupied areas for at least 12 hr. These contrasting patterns suggest that while cheetahs perceive lions as a threat, they are able to avoid them behaviourally, thus minimising the need for long-term spatial avoidance and the subsequent loss of access to resources" (Swanson et al 2016 p8539).

7.3. PRAIRIE DOGS

"Interspecific competition – ie: reciprocal negative effects of one species on another – commonly leads to divergence among species in ecology, morphology, behaviour or physiology, with reduced competition the outcome" (Hoogland and Brown 2016 p1). But "interspecies killing of competing individuals unrelated to predation" (IK) can happen (Hoogland and Brown 2016). If the victim is smaller than the attacker, then there will be evolutionary pressure on the victim to diverge.

IK stills continues in species with size differences as in those studied by Hoogland and Brown (2016) in Colorado, USA - white-tailed prairie dogs (Cynomys leucurus) (herbivores; 500-1100 g as adults) killing of Wyoming ground squirrels (Urocitellus elegans) (herbivores; weighing 200-500 g). Both species have similar diets and share meadow areas. Data for 2007 to 2012 at one site were available (over 30 000 person-hours of observations).

A total of 101 IKs were observed by 47 tagged

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[29] Suppressed smaller predators are also called "competition refugees" (Durant 1998), and forced into marginal habitats.

prairie dogs. A small number of kills involved minor consumption of the victim (23%). No observations of adult prairie dogs killing each other, nor a squirrel killing a prairie dog.

Females who killed more than one squirrel (n = 19) had a significantly better annual and lifetime reproductive success (defined as at least 50% of offspring survival until adulthood) than non-killers, while other variables, like female's age, body mass, and aggressiveness with other prairie dogs did not predict annual or lifetime reproductive success. "Mean lifetime fitness was almost three times higher for serial killers than for non-killers" (Hoogland and Brown 2016 p4).

Hoogland and Brown (2016) summed up: "White-tailed prairie dogs commonly kill Wyoming ground squirrels, and killing enhances both annual and lifetime fitness for female prairie dogs. This is the first demonstration that IK increases fitness for animals living under natural conditions. The number of IKs by a female prairie dog was the only significant predictor of both her annual and lifetime fitness that we could identify during our long-term study. Killing was a stronger predictor of lifetime fitness than even longevity, which is the major factor that affects lifetime fitness for many species. In general, the benefits of killing increased with the number of ground squirrels slain, with female serial killers accruing higher annual and lifetime fitness than one-time killers" (p5).

Because squirrels and prairie dogs eat the same vegetation, IK increases the availability of food for the mother and her offspring. "Sustenance from consuming ground squirrels is thus unlikely to be a benefit of IK, or a reason for its occurrence" (Hoogland and Brown 2016).

There is an alternative interpretation of the findings, "that some prairie dogs inhabit higher quality home territories (eg: those containing more high-quality vegetation), which attract more ground squirrels. With more ground squirrels present, IK probably becomes more likely simply because encounters with ground squirrels are more frequent. In this scenario, the higher fitness of killers results from high-quality vegetation per se rather than from IKs per se" (Hoogland and Brown 2016 p5). This is probably not the case as the female's body mass (which would be higher with good-quality vegetation) was unrelated to reproductive success (Hoogland and Brown 2016).

From the ground squirrels' perspective, why have they not diverged (eg: moved away from prairie dogs)? There are benefits that probably outweigh the costs of IK, including high-nutrition vegetation, the use of empty prairie dog-burrows, and the vigilance of prairie dogs and their alarm calls for multiple predators. "Living with prairie dogs thus involves a compromise for ground squirrels: they incur higher mortality from IK, but they probably incur lower mortality from predation. Consequently, ground squirrels probably receive a net benefit from living with prairie dogs, and perhaps for this reason natural selection has not led to clear character displacement that would reduce competition with prairie dogs" (Hoogland and Brown 2016 p5).

7.4. MIGRATION

Long-distance animal migrations are "repeated seasonal movement from one discrete area to another... [which]... reflect the fitness advantage of seasonally tracking habitats that vary in their distribution of resources, environmental conditions, intra- and inter-specific competition, predation, gene flow, and parasites" (Joly et al 2019 p1). Major terrestrial migrations involve the caribou in the Arctic, and blue wildebeest in the African Serengeti. But are these the longest terrestrial migrations?

The answer depends on how migration distance is measured (Joly et al 2019). One method is "total cumulative annual distance" (TCAD), which is "the sum of the distances between successive positional locations over the course of a year" (Joly et al 2019 p2). Though it is a simple, repeatable method, "it is an estimate of movement distance: all movements, not just migratory ones" (Joly et al 2019 p2).

An alternative technique is the straight-line, round trip distance (RTD) between migration end points. It is "perhaps the most repeatable, versatile, and straight-forward means to measure migration distance. Furthermore, RTD can also be directly compared with historic studies that identify, for example, wintering and calving grounds without recourse to collar-based data. Much like TCAD, RTD varies among individuals within years, among years for the same individual, with changes in population size and density, with differences in seasonal range fidelity, and with new barriers to migration over time" (Joly et al 2019 p2).

Joly et al (2019) compared the RTD and TCAD methods for long-distance (ie: >300 km) large mammal migrations, which are not impeded by human footprints (eg: roads; fences; other human infrastructure and disturbance). Data were taken from existing studies.

Caribou and reindeer had the longest RTD (1200 - 1350 km), while a male grey wolf in Mongolia had the greatest recorded TCAD (over 7000 km). Among nomadic species, the khulan (Mongolian wild ass) (figure 7.2) had a TCAD of more than 6000 km. These prey are tracked by their predator, wolves, and this explains the TCAD of the grey wolf. Wolves tracking the caribou and reindeer also covered long distances.

(Source: Brockhaus (1911); http://www.zeno.org/Brockhaus-1911/I/bkklasi4; in public domain)

Figure 7.2 - Drawing of khulan.

Shellard and Mayor (2020) distinguished between "collective migration" (ie: "the movement of groups whereby individuals both move in concert with one another and affect each other's behaviour"; p1), and "individual migration" (ie: solitary and not influenced by others). Collective migration produces interactions between individuals and emergent behaviour (eg: patterns of movement by birds in a flock).

As animals have to relocate to new food sources, collective migration provides protection from predators and an enhanced chance of survival for the individual.

Shellard and Mayor (2020) observed: "It has long been noted in animals that there is a remarkable degree of long-range organisation that cannot be apparent to each individual, meaning there must be some degree of leadership or communication" (p1). Leaders and followers can emerge in some groups, while, in other cases, "directed movement is imparted by each individual knowing how much local food there is" (Shellard and Mayor 2020 p7).

The study of collective migration suggests three rules that mean that leaders are not necessary (Shellard and Mayor 2020):

i) Repulsion - behaviour that causes individuals to avoid contact with their neighbours.

ii) Attraction - at the same time, behaviour that causes individuals to steer towards the centre of mass of the group.

iii) Alignment - neighbours co-ordinate motion and move in the same direction.

Bialek et al (2012) calculated that starlings, for example, assess their orientation from the six or seven closest birds.

7.5. SEA TURTLES AND NAVIGATION

Animals navigate across vast distances, and in the case of oceans, there are few landmarks, so routes may not be direct. This is the case with green sea turtles (Chelonia mydas) migrating to feeding grounds in the Indian Ocean.

Hays et al (2020) recorded with satellite tags the migration of thirty-three female turtles from their nesting beaches of Diego Garcia (Chagos Archipelago, British Indian Ocean Territory) to isolated islands in the western Indian Ocean (in 2012, 2015, 2017 and 2018). The route travelled was compared to the direct routes of computer simulations. The average distance of the simulations was 2000 km compared to 2700 km by the real turtles.

The real turtles moved towards a single heading and then made course corrections in the open ocean, but "the final stages of finding isolated islands and submerged banks surrounded by deep water often involved protracted search-like movements" (Hays et al 2020 p3239). There was evidence of overshooting the target and then doubling back.

Hays et al (2020) explained: "Taken together, our findings show that turtles lack the ability to always locate small isolated targets with pinpoint accuracy, being, however, able to correct their routes even in the open ocean far from land. Individual-based models revealed that these imperfect routes and course corrections, often far from land, are not because ocean currents carry individuals off route, but rather because turtles often swim on headings that are only approximately, not precisely, target oriented" (p3241).

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