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Some Animals

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

A complete listing of his writings at http://psychologywritings.synthasite.com/. See also material at https://archive.org/details/orsett-psych.

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1. COLOUR VISION OF ARTHROPODS

1.1. COLOUR VISION

Colour vision varies across the animal kingdom from non-existent (colour blindness) to high complexity. Where present it "allows animals to extract information from the spectral composition of light reaching the eyes, by comparing the number of photons in different spectral ranges absorbed by photoreceptors differing in spectral sensitivity and subsequent neural processing" (Yilmaz et al 2022 p1).

Yilmaz et al (2022) continued: "The dimensionality of colour vision is defined by the number of receptor types that provide input into colour processing. As in vertebrates, di-, tri- and tetra-chromatic colour vision (based on two, three and four receptor types, respectively) has been described in arthropods. Spectral information — seen as colour — is found everywhere. The sky changes colour over the day and differs in colour between its solar and anti-solar half. Water bodies change colour with depth and scattering particles, the predominantly green colour of vegetation stems largely from the absorbance spectrum of chlorophyll and secondary metabolites, while bird feathers, the cuticle of arthropods, wing scales of insects and integuments of other animals can produce colour by combining structural mechanisms and pigments. Finally, colourful flowers and other plant structures stand out from the green foliage" (pp1-2).

There are different types of photo-sensitive pigments, but animal vision is "almost exclusively based on photo-pigments in which an opsin — a light-sensitive G-protein coupled receptor —binds a vitamin A-derived chromophore" (Yilmaz et al 2022 p2) [1]. Great variety occurs in arthropods, from a single opsin in deep-sea

[1] "At the population level, studies detecting genetic variants of opsins under selection have provided insights into the genetic basis of local adaptation to light environments and speciation" (Lienard et al 2022 p3).

crustaceans to up to fifteen in some somatopod crustaceans (eg: mantis shrimp [2]) (Yilmaz et al 2022) [3].

Furthermore, opsin genes can be expressed in different eye types (eg: single or compound), and at different times in development, while psin-based pigments vary in spectral sensitivities (eg: to include UV light sensitivity; appendix 1A). Colour vision also involves neural circuitry (eg: specific areas of the brain) (Yilmaz et al 2022).

Colour vision evolved for its function - the "reliable detection, discrimination and recognition of relevant objects" (Yilmaz et al 2022 p4) - most notably to find food and avoid predators.

1.2. BEES

Hempel de Ibarra et al (2022) asserted: "Since bees are completely dependent on flowers as food sources across all stages of their life, they easily memorise colours and other floral cues" (p1). This was shown in experiments where honeybees had a choice of two stimuli (coloured paper).

Firstly, the bees were trained to choose a training pattern with a sucrose reward. Then in two experiments they were offered various concentric patterns of two colours (rewarded) or a single colour (unrewarded). The bees showed a variety of responses (depending on whether they were trained or not) which suggested that they recognised and discriminated patterns. "The variability of floral designs and the bees' flexibility in recalling colour and spatial information suggest a role for colour vision in pattern processing" (Hempel de Ibarra et al 2022 p1) (appendix 1B.

1.3. ANTS

Yilmaz and Spaethe (2022) concentrated on ants and their colour vision. A number of methods have been used to study diverse species:

i) Physiological - eg: the photo-receptor types

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[2] "Mantis shrimps can discriminate both human-visible and ultra-violet colours, but with limited precision compared to other colour-vision systems" (Cronin et al 2022 p1).

[3] "Visual opsins of vertebrates and invertebrates diversified independently and converged to detect ultraviolet to long wavelengths... of green or red light. In both groups, colour vision largely derives from opsin number, expression patterns and changes in amino acids interacting with the chromophore" (Lienard et al 2022 p1).

within the retina or visual pigments present.

ii) Electro-physiological - To measure the firing of cells in response to different coloured visual objects (eg: some species most sensitive to green). Measurements can be taken of cells in the retina (electro-retinography) or in areas of the brain.

iii) Behavioural - For example, the use of a dual choice experiment, where ants are offered beads of different colours to use in nest building. Carbaugh et al (2020) found that the red imported fire ant preferred red over yellow, and green over blue. But this study "did not exclude the possibility that ants might have used achromatic cues for their choices because the control experiments (eg: for brightness or receptor-specific sensitivity differences) were not performed" (Yilmaz and Spaethe 2022 p5).

A similar method involves training ants on a Y-shaped maze where one coloured arm is rewarded and the other not. Yilmaz et al (2017), for example, found that Camponotus blandus workers could discriminate between UV and blue light, and between UV and green light.

Yilmaz and Spaethe (2022) concluded that "the findings across species are variable and inconsistent, suggesting that our understanding of colour vision in ants and what roles ecological and phylogenetic factors play is at an early stage" (p1).

1.4. THRIPS

Thrips are a group of around 6000 species of small fringed-winged insects (figure 1.1) "with highly diverse ecologies, including herbivores that feed on plant tissue and pollen (sometimes also acting as pollinators), fungivores, predators, parasites, and even eusocial and sub-social species, some of which are gall-forming" (Lopez-Reyes et al 2022 pp1-2).

The behavioural study of colour vision uses traps of different colours, and counts the number of thrips caught (ie: attracted to that colour) (as developed by Lewis 1959). "A synthesis of the literature describing colour preferences confirms that many species of thrips are attracted by colour, but not all colours are preferred equally, and preference varies between species, populations and experimental conditions" (Lopez-Reyes et al 2022 pp3-4).

Colour preference can be variable by season, for instance. "For example, Thrips angusticeps shows strong attraction towards yellow colour before flowers bloom and then changes preference towards blue and white when flowers are in full bloom. In addition, there is some evidence suggesting that the response of thrips to colour could also be correlated with light fluctuations between different times of year" (Lopez-Reyes et al 2022 p7).

Two key facts remain undetermined, for Lopez-Reyes et al (2022), which are "how good thrips colour discrimination is and whether they indeed possess true colour vision" (p7).

(Source: Sikander Kiani; public domain)

Figure 1.1 - Preserved specimen of thrip.

1.5. NOCTURNAL INSECTS

The nocturnal world may appear black and white to humans because of our visual system, but for those animals that can see, "the world is as equally colourful at night as it is during the day, "and the advantages of colour vision — for recognising food, mates, habitats or homes — are equally great at night as they are during the day. Nonetheless, due to the problems of visual noise in very dim light, the discrimination of colour at night is far from trivial, and not surprisingly this ability is rare among animals" (Warrant and Somanathan 2022 pp1-2) [4].

Light is present at night in the form of moonlight and starlight (as well as the artificial illumination of humans).

Some pollinators have nocturnal colour vision as a number of flowers open at night. Four species have been confirmed, including the elephant hawkmoth, and the carpenter bee (Warrant and Somanathan 2022).

The basic experimental method used to study colour vision in insects involves training the them to associate a particular coloured target with a food reward, then to present that colour among others. For example, Kelber et al (2002) trained the elephant hawkmoth with blue and yellow rewarded targets, and then tested them at light levels from 20-30 minutes after sunset to dim starlight. At all light levels the moths were at least 80% accurate in finding the coloured target among grey ones.

This research also showed evidence of "colour constancy" (ie: the ability to perceive an object as the same colour under different lighting). Moths were trained to associate food with either a green or turquoise target under white illumination, then they were tested under white or yellow illumination. The moths had "no problem distinguishing the rewarded colour from the unrewarded colour either under the white illumination or under a yellow-shifted illumination" (Warrant and Somanathan 2022 p10).

Artificial light created at humans at night is being found to impact nocturnal insects. Artificially lit meadows were visited less by pollinators than dark meadows (Knop et al 2017). Warrant and Somanathan (2022) considered the possible explanations: "Nocturnal pollinators, such as moths, might simply be lured away from flowers by an artificial light source, or they may even be negatively impacted by some specific physiological reaction to the light source that causes

[4] Note that "the physical 'colour' of an object — that is, the spectrum of light reflected from its surface — depends essentially on two things: (i) the spectrum of irradiance and (ii) the spectral reflectance properties of the object's surface (which remain constant). Exactly how an animal perceives this 'colour' depends on how the visual system is built" (Warrant and Somanathan 2022 p2).

temporal disruption of developmental processes, spatial disorientation or visual disruption. Alternatively, changes in the attractiveness of the flowers themselves might also be responsible for visitation decline" (p13).

1.6. APPENDIX 1A - REINDEER VISION

Living in the Arctic means dealing with extremes in light as well as temperature. It has found that the eyes of reindeer change to deal with the seasonal light conditions (Robson 2022).

At the back of the eyeball in many animals is the tapetum lucidum ("a biological mirror"; Robson 2022), which reflects back light through the translucent retina. This allows animals to make the most of low light levels. Hogg et al (2011) found high sensitivity to the ultraviolet (UV) range of light. During the polar winter, the sun is out of sight, but there is a kind of twilight (containing UV light). Reindeer eyes have evolved to perceive this light (Robson 2022).

The ability to see UV light is only needed for half the year, so the tapetum changes colour in the summer (daylight) months (Robson 2022).

1.7. APPENDIX 1B - BEES OR WASPS

In the public imagination, even as far back as Aristolte 2000 years ago, bees are viewed positively while wasps are not. Simms (2022) considered the two insects on different criteria:

i) Communication - Both bees and wasps communicate in a variety of ways (eg: vibrations; chemical), but the "waggle dance" of the honeybee has a sophistication beyond any wasp species.

ii) Cognition - Both bees and wasps show sophisticated cognitive skills (for the size of their brains) in different ways, particularly in laboratory experiments, though more studies have been performed with bees. Highlights include a basic grasp of numbers by bees versus transitive inference by a species of paper wasp. Transitive inference is shown when told that "A is larger than B", and "B is larger than C", being able to infer that "A is larger than C".

iii) Building skills - A variety of building materials and skills used by both insects for their nesting.

iv) Usefulness to humans - Pollination is the main usefulness of bees (and honey-making), while some wasps also pollinate, but mostly they act as pest controllers of woodlice, spiders, caterpillars, aphids, and flies.

v) Cunning - Kleptoparasitism (ie: stealing food) is performed by certain bees, while common wasps raid honeybee hives, for example. The dementor wasp is able to inject venom into cockroaches, which "zombifies" them, and they are kept as "living food" for the offspring.

vi) Navigation skills - More experiment work on bees, which shows their ability to navigate several miles. But wasps also show similar abilities where studied (eg: European bee wolf).

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2. A FIRST REPORT OF OCTOPUS THROWING OBJECTS

"The throwing of objects is an uncommon behaviour in animals" (Godfrey-Smith et al 2022 p1). Throwing with a particular aim has even been seen as "distinctively human", but there are a few cases observed in animals (table 2.1) (Godfrey-Smith et al 2022). Throwing at a target could be viewed as "a form of tool use" (Godfrey-Smith et al 2022 p2).

Study	Species	Behaviour
Goodall (1964)	Chimpanzee	Sticks, stones, leaves at humans and baboons
Wickler & Seibt (1997)	Elephant	Mud, soil, vegetation at rhino
Falotico & Ottoni (2013)	Capuchin	Stones at capuchins

(After Godfrey-Smith et al 2022 table 1)

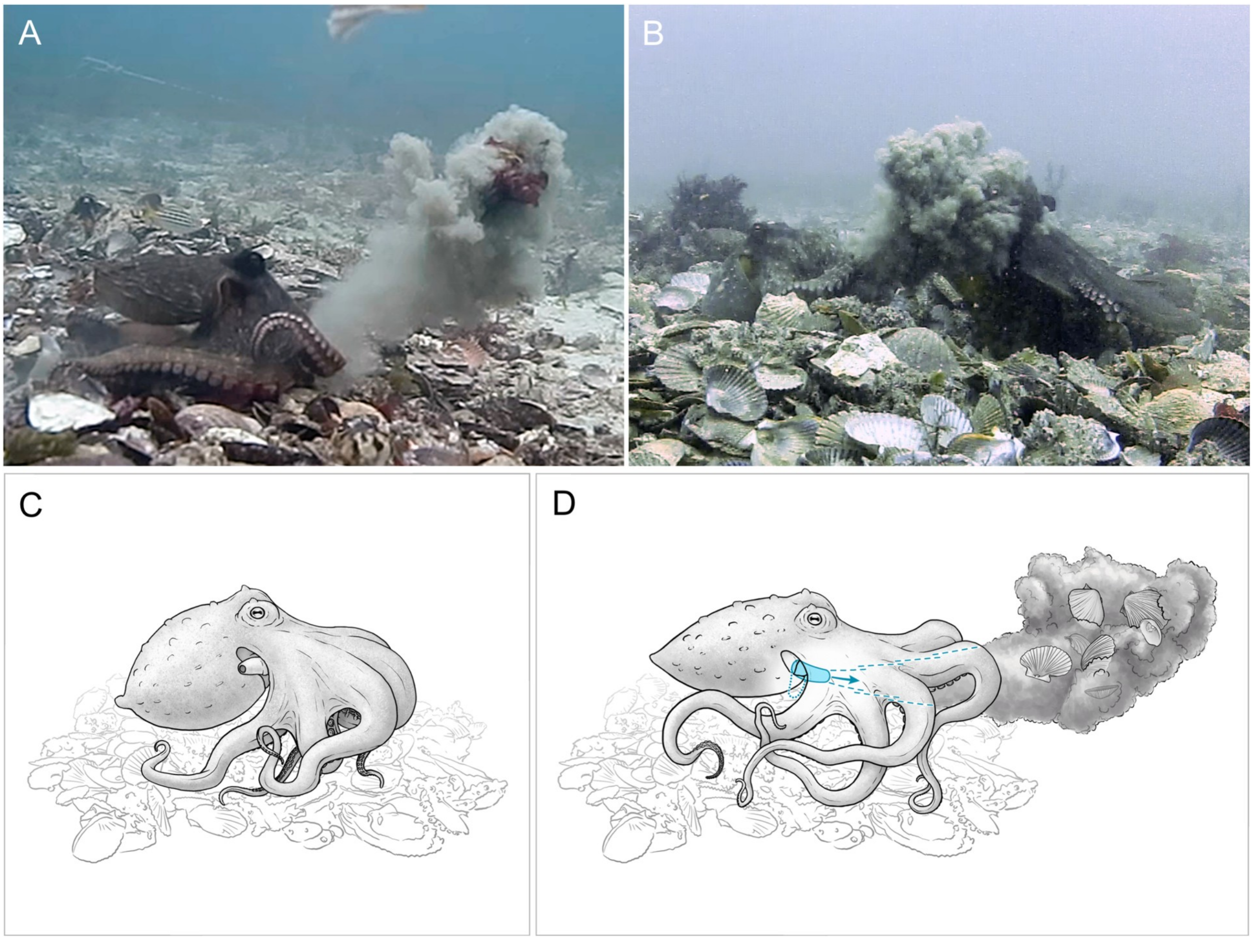
Table 2.1 - Examples of animals throwing.

Godfrey-Smith et al (2022) reported, for the first time, the gloomy octopus (Octopus tetricus) throwing debris. The data came from Jervis Bay, North South Wales, Australia. "Shell throws" were first observed informally, and then video recordings were made in 2015 (over 21 hours and 102 throws).

Octopuses were seen to gather material (shells, silt and algae) in their arms, and then use their siphon to expel the material under pressure as part of a water jet (figure 2.1). Godfrey-Smith et al (2022) explained: "We interpret these behaviours as throws. The behaviour could equally be described as an arm-guided release of material propelled... by force arising from the jet" (p5).

Shells were thrown most often, and throwing was more often in interactive contexts. There was seventeen "hits" recorded. A hit was defined as "if another octopus interrupted the motion of the thrown materials (shells or algae contacted the octopus) or when thrown silt enveloped part of another octopus" (Godfrey-Smith et al 2022 p3) (figure 2.2).

Was the throwing at a target intentional or part of den maintenance and food waste removal behaviours? Throws that hit other individuals were different (eg: from



(A = Octopus projects silt and kelp from video; B = An octopus is hit by a cloud of silt projected through water by throwing octopus from video; C = Drawing of octopus collecting materials before throwing; D = Drawing of throwing) (Video by Peter Godfrey-Smith; drawings by Rebecca Gelernter)

(Source: Godfrey-Smith et al 2022 figure 1)

Figure 2.1 - Debris throwing by gloomy octopus.

between the most foremost arms and/or evidence of body orientation towards the target). "Hits in many cases also occurred within sequences of interactions that featured ongoing mild aggression (arm probes and momentary grappling). The octopus who was hit often altered its behaviour in anticipation or reaction to a throw; octopuses in the line of fire ducked, raised arms in the direction of the thrower, or paused, halted or redirected their movements" (Godfrey-Smith et al 2022 p8).

The researchers accepted that "[S]howing intention in a behaviour is difficult in non-human animals"

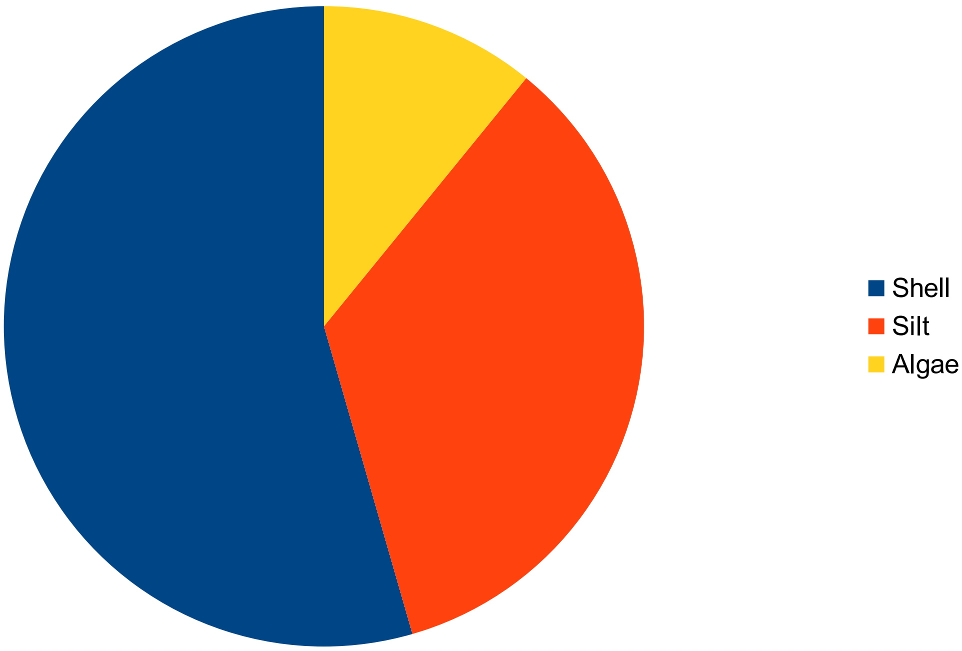


Figure 2.2 - Proportion of throws of each material.

(Godfrey-Smith et al 2022 p9) [5].

The video recordings provided a limited amount of data. The researchers admitted the key things that they had not seen in the videos or in other observations: "We have not seen an octopus who was hit by a throw 'return fire' and throw back. We have not seen a hit directly initiating a fight, due to immediate retaliation by the target. The general effects of throws were difficult to assess, and we were hampered by the limited number of hits. Some throws in what appear to be fairly intense interactions were not directed at another octopus but into empty space" (Godfrey-Smith et al 2022 p9).

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[5] In studying animals, Gutnick et al (2023) explained, "linking brain activity to behaviour is done by implanting electrodes and directly correlating electrical activity with observed animal behaviour. However, because the octopus lacks any hard structure to which recording equipment can be anchored, and because it uses its eight flexible arms to remove any foreign object attached to the outside of its body, in vivo recording of electrical activity from untethered, behaving octopuses has thus far not been possible" (p1171). These researchers, however, were able to implant a portable data logger under the skin with electrodes attached to the brain of an octopus. This logged data (electro-physiological - ie: electrical brain activity - and motion) for up to twelve hours, and the recordings could be subsequently synchronised with video recordings of behaviour.

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3. ELEPHANTS

3.1. INTRODUCTION

Among the three species of elephant - Asian (Elephas maximus), African savannah (Loxodonta africana), and African forest (Loxodonta cyclotis) - females are central to the social structure. "These groups are multi-levelled with older females exhibiting dominance over younger ones, and social organisation is maintained by fission-fusion processes. Upon reaching sexual maturity, male elephants remain on the periphery of these female-centred groups; younger males often form social relationships with each other before becoming more solitary at their sexual peak. Male and female elephants are generally spatially segregated, except during periods of reproduction when females are in oestrus and/or males are in a heightened reproductive period called 'musth'" (Schulte and LaDue 2021 p2).

Males in musth "dribble urine, secrete an odorous, viscous fluid from the temporal gland (ie: temporal gland secretions, TGS), can act aggressively, and focus their energies on locating receptive females" (Schulte and LaDue 2021 p2). Females are in oestrus for a few days every 4-5 years, while musth is more regular. So, chemical signals are key to breeding. Such signals are also important in food selection and predator detection (Schulte and LaDue 2021).

A pheromone, frontalin, has been found in TGS, as well in blood, breath, and urine. Flehmen is where the chemical in the substrate is transferred by the trunk to the openings of the vomero-nasal organ in the roof of the mouth. This behaviour has been used as a measure of interest in the opposite sex's urine (Schulte and LaDue 2021).

In terms of predator detection, elephants are relatively safe, except from large cats and humans. There are studies that show the use of olfactory, visual, and auditory cues. For example, Bates et al (2007) presented African elephants with clothing worn by Maasai and Kamba tribesmen. The "response to the Maasai clothing was more aggressive, perhaps reflective of the increased threat by this tribe in which a rite of passage for men involves spearing an elephant" (Schulte and LaDue 2021 p7). While elephants could distinguish the sounds of large cats from control sounds (eg: Thuppil and Coss 2013), and the presence of lions from the smell of their dung (even semi-tame African elephants; Valenta et al 2021).

Chemical signals in the form of plant volatiles are used in foraging decisions, as well as detecting water using olfactory cues (Schulte and LaDue 2021).

3.2. TRUNK BEHAVIOUR

In response to chemical signals on the body, elephants show trunk to scent emitting organ (SEO) behaviours - ie: "close physical contact is initiated by the subject directing its trunk towards a target elephant's mouth, temporal gland or genitals" (Allen et al 2021 p2). Allen et al (2021) studied this behaviour in male African savannah elephants, who live in loose associations, and the behaviour has been labelled as "greetings".

Greeting behaviours that involve inspection of the body areas emitting scent has been reported in other species (eg: armpit and genital sniffing by howler monkeys; inspection of anogenital areas by spotted hyenas) (Allen et al 2021). Meeting of strangers or reunions have the potential for conflict for individuals, and greeting behaviours "can communicate their intention to interact in an affiliative manner, as well as update previously insecure relationships (eg: establish relative dominance status) via close contact assessments" (Allen et al 2021 p3).

Allen et al (2021) collected data along the Boteti River in Makgadikgadi Pans National Park, Botswana, between September 2015 and 2018. Focal observation was used - one individual was observed (video-recorded) for the duration of their stay at the observation point. Observation segments of ten minutes were distinguished (n = 1223, involving 240 individuals). The elephants were categorised by age into adolescents (10-15 and 16-20 years old), and adults (21-25 and 26 and above years old) based on shoulder height and overall body size. Trunk-to-SEO behaviours were scored independently by three researchers.

Adolescents performed trunk-to-SEO behaviours significantly more than adults, and trunk-to-mouth was most common of the body areas. Older adults were more likely to reciprocate the behaviour. The behaviour was more likely to be targeted at a male of similar age. The behaviour did not appear to be a greeting as there was "no change in an elephant's probability of directing a trunk-to-SEO behaviour over the time course of his stay at a hotspot, nor any evidence that elephants directed these behaviours more upon their initial arrival at hotspots" (Allen et al 2021 p10).

The fact that adolescents showed the behaviour at a higher rate may be part of their learning of social networks. Allen et al (2021) explained: "As adolescents are more likely to be recently dispersed from their natal herd, they may have a greater need to obtain information about other males in the male social network, including identities of individuals, and relative dominance rank, compared to adults that are more established and stable in the network. Similarly, adolescent male African elephants are more sociable in general than adults, and may perform more of these trunk behaviours to assist in establishing new contacts and initiating further affiliative interactions with social companions, a pattern also seen in other species that perform greeting behaviours" (p11). Assessment of sexual status was not seen as the reason for the behaviour because the mouth was the main focus of the trunk.

Allen et al (2021) ended: "Our results suggest male elephants may use trunk-to-SEO behaviours to facilitate further positive interaction with other males or assess aspects of phenotype (such as relative dominance) between males generally occupying the same ecological space, rather than as a benign 'first contact' signal directed at novel social partners" (p14).

3.3. GREETING BEHAVIOUR

African elephants in zoos have been moved around the world to manage viability over the years. So, it is possible that related animals that were separated will be brought back together. This is reunification, and involves different behaviours to strangers meeting. Related animals show the so-called "Greeting Ceremony" (Poole et al 2011) (eg: touching trunks; opening mouth; loud vocalisations) (Horner et al 2021).

Horner et al (2021) observed the reunification of two mother-daughter pairs that had been separated for two and twelve years, and two unifications of unrelated elephants. The elements of the Greeting Ceremony were shown by the related animals, suggesting recognition of kin, while the meeting strangers showed more agonistic behaviours (eg: shaking the head; showing dominance or servility). The most obvious difference was seen in the first contact of trunks - three seconds (on average) for related animals compared to 102 625 seconds for strangers.

3.4. VOCAL COMPLEXITY

The "social complexity hypothesis" (SCH) (Freeberg et al 2012) proposes that complex social relationships between individuals in a group drive the evolution of complexity in communications. "The underlying notion is that animals living in highly variable and complex social environments (eg: individuals interacting frequently and in diverse ways), need to convey a broader range of information to coordinate their social interactions. Such increased expressiveness can be achieved via various mechanisms, including an increase in vocal repertoire size and acoustic variation within and between call types, as well as the combination of call types into larger utterances" (Hedwig et al 2021 p2).

Hedwig et al (2021) investigated the SCH in relation to elephants, and in particular in forest and savannah species of African elephant. The two species vary in social complexity, and so should show differences in communicative complexity, according to the SCH.

Forests elephants live in small groups of an adult female and her dependent offspring, while savannah elephants "exhibit complex multi-tiered fission-fusion societies, in which family units, consisting of a matriarch, her offspring and her close adult female relatives and their offspring, as well as more extended family 'bond groups' may split and rejoin on a regular basis while maintaining long-term social relationships within extensive social networks" (Hedwig et al 2021 p3).

Rumble vocalisations and other call types (eg: cries, barks, roars) were recorded from forest elephants in Dzanga-Ndoki National Park in the Central African Republic in 2018-19, and savannah elephants in Ambroseli, Kenya (at various times between 1986 and 2020). Behaviour was also observed at the time of calls.

Forest elephants produced rumbles that could be classed as seven distinct contextual categories (eg:

competition; separation; nursing) (table 3.1). This was based on 246 calls while in forest clearings. Applying these categories to the database of 1177 savannah elephant calls, there were differences found. For example, the savannah elephants produced more rumbles in affiliative contexts, while forest elephants rumbled more in separation and competition contexts. "Rumbles used by both species in the same broad contexts appear to be structurally similar" (Hedwig et al 2021 p10).

- Affiliative - given during formation or maintenance of social bonds (eg: greeting-rumble).
- Competition - given during conflict over resources.
- Separation - given when an individual is separated from the group during travelling.
- Nursing - given by calf to initiate feeding or during weaning (eg: begging-rumble).
- Logistics - given to co-ordinate movement (eg: let's-go rumble).
- Anti-predatory - eg: rumble-roar when predator present.
- Sexual - during mating.

(Source: Hedwig et al 2021 table 1)

Table 3.1 - Behaviour associated with different categories of vocalisation.

In terms of call combination (which is same as a sign of complex communication), as compared to stand alone roars, for example. Forest elephants produced more than savannah ones. Adults females in both species produced more call combinations than adult males and young males and females.

Overall, Hedwig et al (2021) felt that the data contradicted the SCH: "The socially less complex forest elephant appears to exhibit communication skills that are at least as sophisticated as savanna elephants, a species with one of the most complex social systems observed among mammals. Comparison based solely on the acoustic structure of rumbles of both species indicates a seemingly larger but equally highly graded repertoire of rumble types in forest elephants as compared to savanna elephants" (p14).

The researchers, however, accepted that the recordings and observations of forest elephants were much less than of savannah elephants, and were specific to one clearing in a dense forest. The savannah elephants were recorded on open grasslands.

3.5. FORAGING BEHAVIOUR

Elephant, like the hippopotamus and rhinoceros, are "mega-herbivores", and they are "well known for their role in ecosystem engineering. Elephants perform important ecological roles, such as affecting the quality of foliage available through their foraging activities. Furthermore, they modify vegetation structure, generally by decreasing the amount of woody vegetation (which can aid in preventing bush encroachment); and additionally aid in seed dispersal" (du Plessis et al 2021 p2).

The specifics of foraging behaviour were observed among six male African savannah elephants in the Kruger National Park, South Africa, from June 2007 to 2008 (du Plessis et al 2021). Twice per week, each individual was observed for at least thirty minutes continuously (a total of over 400 observation periods).

Foraging (ie: browsing and grazing) occurred more often before than after (ie: the warmer part of the day), and resting was the opposite. This was similar to a study of eighteen elephants in Uganda (Wyatt and Eltringham 1974).

Grazing (ie: actual eating) occurred more during the wet season, while browsing (ie: looking for appropriate food) was more common in the dry season. The nutritional value and digestibility of grass, for example, varies between the seasons.

More time was spent foraging when a bull was alone or with other bulls as compared to with females. "Elephants usually form same-sex groups; when adult male elephants are associated with females, it is usually only for short periods of time, and for reproductive purposes when females are close to or in oestrus" (du Plessis et al 2021 p9). However, musth did not alter significantly the overall time spent in foraging. But another study (Poole 1989) did find that elephants in musth spent less time foraging and more time looking for females. Note that "musth can also be divided into different stages; pre-musth, musth, and post-musth. It is possible that elephant bull foraging levels may be differentially affected depending on the specific stage of musth within which the bull finds itself..." (du Plessis et al 2021 p10). The researchers accepted that their sample size was small.

Overall, du Plessis et al (2021) showed seasonal and social factors influences on foraging behaviour. Studies of other animals in the area have reported similar differences. For example, adult male African buffalo in mixed herds forage less than females and young males, while impala vary their foraging between seasons (du Plessis et al 2021).

3.6. DROUGHTS

Droughts impact grazing species like elephants as a short or non-existent growing season means reduced vegetation. Droughts can also lead to the loss of experienced individuals and the consequences of that.

Lee et al (2022) analysed data collected since 1972 on a population of elephants in the Amboseli region of Kenya (over 3700 recognised individuals). A drought year was defined as more than six consecutive months with less than 20 mm of rain, and a total annual rainfall of less than 250 mm.

In extreme drought (eg: 2008 and 2009), calves under two years of age and females over forty years were more likely to die. Calves that survived drought, however, were more likely to die early (16.8 years vs 24.9 years median longevity for males, and 27.4 and 37.6 years respectively for females). "Most natural deaths during droughts appeared to be the direct result of the drastic food limitation, possibly increasing susceptibility to other illness or infection, rather than starvation alone. Social disruption due to the loss of the matriarch also increased the probability of death for calves; whether this was related to loss of knowledge, loss of access to prime foods, reduced competitive ability with undisturbed families, or less protection for calves... remains to be determined" (Lee et al 2022 p414).

A drought had mixed effects on the age of reproduction. For example, "there were no persisting early drought effects on female age at first conception while matriarch loss around puberty accelerated reproductive onset. Experience of an early life drought did not influence age-specific reproductive rates once females commenced reproduction" (Lee et al 2022 p408). But, for males, leaving the family (independence) was delayed in some cases, but earlier in others, and no impact on age of first musth. "Fertility and musth onset were not directly impacted by adverse experiences that occurred in the first 2-5% of a lifespan, but were affected by the demographic consequences of such events; smaller cohort sizes and fewer competitors" (Lee et al 2022 p416).

This study was an extension of Lee et al (2013), who had analysed data for 2652 elephants in Ambroseli where the birth date was known. The analysis of early experiences included drought during gestation, and separation during peak lactation (first 24 months of life). Both drought, and maternal inexperienced (ie: first born calf) impacted calf survival. "Being born in a drought period to an inexperienced mother has adverse consequences for longevity, adult size and reproductive potential" (Lee et al 2013 p4).

3.7. OBSERVATION OF RARE BEHAVIOUR

Pokharel et al (2022) stated: "A 'rare' behaviour might simply be one that occurs at low frequencies relative to other behaviours or is difficult to observe directly due to unfavourable field conditions (for instance, terrain, dense vegetation, and aquatic environment limiting visibility and navigation) or animals' elusiveness. A detailed description of rarely observed behaviours (parturition, death, reciprocity, sleep) requires the observer to be at the right place at the right time. With appropriate caution and interpretation, rare events and anecdotes can provide valuable insights into a species' life-history traits and thus lead to advances in behavioural theories" (p2). Famous examples of discoveries of rare behaviours include tool-use by chimpanzees (eg: Kummer and Goodall 1985), and the response of various animals to their dead (known as thanatological behaviour).

Pokharel et al (2022) concentrated on the latter and elephants. Among African savannah elephants, these researchers, explained, "several studies have documented strong interest in dead conspecifics (expressed by investigating, repeatedly visiting or touching the deceased, as well as self-directed reactions), irrespective of their genetic relationship with the dead individual. They show greater inquisitive behaviour towards deceased conspecifics than heterospecifics. A study on African elephants showed that the herd members reacted to playback calls of former members (a dead female that had died during the study and another female that had left the natal herd) suggesting long-term memory and vocal recognition of individuals [McComb et al 2000]" (p2).

Pokharel et al (2022) hoped to learn about Asian elephants here, as the information is lacking, by using YouTube videos. "Compared to African savannah elephants, Asian elephants live in relatively small groups with weaker and non-linear dominance networks among social units, and associations between females that tend to be temporally stable across seasons and years" (Pokharel et al 2022 pp2-3).

Thirty-nine relevant videos (covering 24 cases) were found between May 2020 and June 2021, and the researchers coded for multiple variables (eg: approaching the dead carcass; sniffing; shaking of the dead individual; touching with trunk).

"The most common thanatological behaviour by elephants in this study was the touch response. Responders repeatedly touched the body parts of the deceased using the trunk and the legs. Other touch responses included trunk rest, tapping and shaking the trunk or leg of the deceased, and climbing on and mounting-like postures on the dead body (by young individuals). Touching the corpse was also the most frequently observed behaviour in African elephants" (Pokharel et al 2022 p13). Approaching a corpse or dying individual was also observed in the videos.

There were five cases of elephants carrying dead calves in the videos. But it was not possible to establish the relationship of the individuals (which is usually the mother carrying the calf in better documented cases in elephants and other species), nor the period of carrying (which has been reported as a few days to weeks in other studies).

The study was able to show similarities between Asian and African elephants in their thanatological behaviours. But, like any observation-based study, it was only possible to describe the behaviour, not explain it or establish causation. Not being physically present to observe also meant details were missed, and the researchers were dependent on the filming (ie: secondary source data).

More generally, the use of digital material on social media sites is a great opportunity for researchers. Jaric et al (2020) has used the term "iEcology" to describe the opportunity.

Table 3.2 sums up the strengths and weaknesses of observation via YouTube videos.

STRENGTHS	WEAKNESSES
1. Vast amount of data available, which is beyond that which a single or small group of researchers could collect. Multiple videos of the same event would be the ideal. 2. Data from parts of the world that researchers cannot or would not go. 3. Opportunistic video capture of rare behaviours by many pairs of eyes (like "citizen science" projects). 4. Little or no cost to the researchers (in terms of collection of data). 5. Easily accessible (via the Internet). 6. Videos can be stopped, slowed down, and zoomed in to help the observers. 7. It is possible to apply the rigour of structured observational methods (eg: coding; point sampling; inter-observer reliability). 8. The use of publicly available material overcomes any concerns about privacy invasion, confidentiality, and so forth.	1. The material is classed as secondary source data, and so is dependent on the recorder's collection. 2. Not observing in person or filling by the researchers misses details (eg: smells; behaviour off camera; environmental and weather conditions). 3. The recorder may have different motivations to the researchers in filming and posting the material. 4. The quality of image (and sound) will vary. 5. The possibility of editing or changing of raw footage. 6. Searching for the appropriate videos depends on the accuracy of tagging and labelling of content. 7. The policy of YouTube (eg: removing certain content). 8. Ethical concerns if the material includes illegal content, or collected illegally.

Table 3.2 - Strengths and weaknesses of observation of animal behaviour via YouTube videos.

3.8. LOSS OF MATRIARCHS

Transmission of knowledge is important in long-living social animals, like elephants, but orphaned elephants show impairments here. "The mother-offspring bond is particularly important, as demonstrated by the reduced survival probability of orphaned elephant calves who lost their mothers early on in life" (Shannon et al 2022 p2). Older females play a key role in the group.

McComb et al (2011) showed the importance of older matriarchs among African savannah elephants in Ambroseli National Park, Kenya in playback experiments with lion calls. "While elephant family groups within a stable, natural study population were consistently able to assess the greater risk associated with three roaring lions versus one, those with older matriarchs were significantly better at the more subtle task of identifying the increased threat associated with male versus female roars (male lions being more than 50% larger and at a distinct advantage in capturing large-bodied prey)" (Shannon et al 2022 p3).

Shannon et al (2022) developed this work by comparing the stable groups in Kenya with orphaned elephants in groups in Pilanesberg National Park, South Africa. Playback involved single lion roars (female and male) and three lions together (male and female). The response of the elephant group was recorded, including bunching (a defensive response).

The elephant groups in South Africa were more likely to show bunching to any lion calls, while the family groups in Kenya responded only to the greater threats (as McComb et al (2011) found previously).

The researchers felt that bunching in response to lion roars was an automatic behaviour, but distinguishing the level of threat was learned with the mother and/or matriarch. Orphaned elephants did not have this opportunity, and so did not learn the finer details. "If populations experience extreme social trauma (eg: through culling, poaching or translocation) then the mechanisms that allow effective knowledge acquisition and transfer between related individuals may be severely disrupted" (Shannon et al 2022 p9).

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4. PREDICTING EVOLUTION

4.1. ISSUES TO CONSIDER

Cano et al (2023) began: "Predicting the dynamics and outcome of evolution is an important goal of the biological sciences, offering the potential to design better drugs, combat pathogens and conserve endangered species" (p1).

But can evolution be predicted? Crocker et al (2023) replied with the traditional view: "Because evolution is shaped by multiple stochastic forces and rare events acting across molecular, population and environmental scales, there has been a sceptical view on the predictability of biological systems" (p1). However, they continued, the advances in genome sequencing and computing may mean an affirmative answer to the question: "New genome editing approaches are opening up new experimental avenues no longer limited by 'chance' [Gould 1989], and these approaches allow us to empirically describe and quantify the types of phenotypic variation generated by genetic variation. In parallel, computational and theoretical approaches are providing new insights in our understanding of these new data and giving us tools to measure the chance events behind evolution. All of these elements are now converging into what we anticipate will become a predictive theory of evolution" (Crocker et al 2023 p1).

Despite the random nature of mutations, there are "mutation biases", which "make some mutational steps to adaptation more likely than others" (Cano et al 2023 p2).

One way to predict evolution is to understand the "mutation spectrum" (ie: the likely range of mutations). But there are variables that complicate this, including hypermutations, and changes in the mutation spectrum but not necessarily in total mutation rate (Cano et al 2023).

Forecasting has the greatest potential in the short and intermediate term. High-quality experimental data are key. "For example, over short timescales, where one may wish to predict the next beneficial mutation to arise and go to fixation, empirical knowledge of the distribution of fitness effects is key, because this provides information about the fixation probabilities of new mutations. At intermediate timescales, where one may wish to predict which of several possible mutational trajectories to adaptation is the most likely, empirical knowledge of the fitness effects of combinations of mutations is key, because this can be used to delineate between mutational trajectories that ascend adaptive peaks from those that fall into maladaptive valleys" (Cano et al 2023 p1).

Crocker et al (2023) outlined three areas for potential predictable evolution:

i) "The predictable genome" - eg: the prediction of disease risk of an individual from knowledge of their genome.

"Epistasis, when biological components interact, is one complication in accurate phenotype prediction, as interactions between mutations add substantial complexity to adaptive landscapes" (Crocker et al 2023 p2).

Epistasis is gene-by-gene interaction (G x G), while there is also gene-by-environment interaction (G x E), and epistasis interacting with the environment (G x G x E). All of these interactions "complicate evolutionary predictions because they alter expected phenotypes or fitness of individuals. Studying their extent and incorporating their effect into evolutionary predictions is daunted by the complexity of the genotype space and the myriad of environments that could be tested" (Ghenu et al 2023 p1) [6].

Ghenu et al (2023) modelled the different types of interactions for Escherichia coli (E-coli) and anti-biotic resistance (ABR) [7]. This included fifteen "fitness landscapes" with single amino acid changes. It was found that epistasis made predictions of evolution more difficult in benign environments (ie: no anti-biotic), but "the effects of ABR mutations are predictable in the presence of an anti-biotic" (ie: an adverse environment) (Ghenu et al 2023 p8).

ii) "Gene-regulation and networks" - Despite the variety in gene expression in a population, there are some variants that persist. "Pleiotropy, the effect of an allele on multiple traits, is thought to enhance

[6] "Adaptive evolution is 'short-sighted', but single-step mutations can elicit long-term consequences. This concept is termed historical contingency [Gould 1989], which describes that the future of a genome's evolution is dependent on its current genomic background" (Horton et al 2023 p2).

[7] Yeast and bacterial populations are highly studied here (Diaz-Colunga et al 2023).

repeatability by constraining the number of available beneficial mutations" (Crocker et al 2023 p2).

Li et al (2023) commented: "Mutations may be largely random, but the loci of evolution are not. Through analysing causal variants underlying natural variation, previous studies have found that some specific genes or nucleotide substitutions are more often used in evolution than others" (p1). These researchers continued: "Therefore, evolution may be predictable if we gain a more comprehensive understanding of the roles of different kinds of molecular changes and their possible contributions to evolution. However, the ability to predict evolution requires a full construction of the genotype-to-fitness map, which is difficult to achieve by analysing naturally occurring variations that are limited in number and shaped by selection" (Li et al 2023 p1).

Data on the fruit fly (Drosophila melanogaster) is growing as this organism is used in many genetic studies, including where genes are deliberately manipulated. The hope is that the pattern of mutations will be understood in terms of the outcome (ie: the phenotype). Put very simple, that mutation A leads ultimately to observable change B (eg: an aspect of flying behaviour).

iii) "Predicting population and community evolution" - Understanding community-level properties may help spot the repeatability of the evolution of such properties.

4.1.1. Epistasis and Fitness Landscape

One type of global epistasis is "characterised by diminishing returns, where the fitness effect of a beneficial mutation becomes smaller in fitter backgrounds" (Diaz-Colunga et al 2023 p2), while another type characterised by increasing costs is "the situation where the deleterious effect of a mutation increases in magnitude when added to fitter backgrounds" (Diaz-Colunga et al 2023 p2). There is also the "increasing returns epistasis" where "a beneficial mutation increases in a predictable manner when added to fitter genetic backgrounds" (Diaz-Colunga et al 2023 p2).

"Reciprocal sign epistasis" is where "two mutations together yield a benefit while they are deleterious separately" (Servajean and Bitbol 2023 p1). Using the concept of "fitness landscapes", they can produce a "fitness valley" as opposed to a "fitness peak". The latter can lead to a situation preventing further adaptation (Servajean and Bitbol 2023) [8].

In a constant environment, where "if mutations are rare, the evolution of a homogeneous population of asexual micro-organisms can be viewed as a biased random walk in genotype space, and thus on the associated fitness landscape" (Servajean and Bitbol 2023 p1). Random walks that only "go upwards in fitness" (p2) are called "adaptive walks" (Servajean and Bitbol 2023).

Servajean and Bitbol (2023) used computer modelling of a homogenous population of asexual individuals to explore the fitness landscape. They found that "early adaptation in rugged fitness landscapes can be more efficient and predictable for relatively small population sizes than in the large-size limit" (Servajean and Bitbol 2023 p1). Such modelling makes a number of assumptions, and holds many variables constant.

While experimental evolution with fruit flies suggests an interesting pattern: "Selected phenotypes consistently respond in a very predicable way, but the underlying allele frequency changes are much less predictable" (Schlotterer 2023 p1).

An example of the experimental work is Barghi et al (2019) who exposed fly cultures to a high temperature regime in the laboratory, and after sixty generations the evolved flies had higher fitness (measured as fecundity) compared to controls. The adaptations were found to last twenty generations when the temperature was reduced to normal (Schlotterer 2023) [9].

4.2. EVOLUTION OF ALTERNATIVE COURTSHIP STRATEGIES

"Under intense natural and anthropogenic selection, adaptive traits can evolve rapidly in the selected populations. However, when behavioural traits are abruptly modified by directional selection, other behaviours that affect fitness might be distorted" (Wada-Katsumata et al 2023 p1).

A good example of natural selection pressure is male Pacific field crickets (Teleogryllus oceanicus), who use acoustic signalling to attract a mate, but the calls also attract a parasitic fly that lays her eggs on the male,

[8] "Transient mutation bias, which operates only on one mutational step, can influence landscape navigability by biasing the mutational trajectory early in the adaptive walk. This sets an evolving population upon a particular path, constraining the number of accessible routes and making certain peaks and routes more likely to be realized than others" (Horton et al 2023 p1).

[9] Two concepts are useful to know - convergent and parallel evolution. The latter "starts from genetically highly similar founder populations and changes in the same direction" (p2), while convergent evolution is change in the same direction from two genetically divergent populations (Schlotterer 2023).

and in time the emerging larvae eat the male. A genetic mutation produced silent male crickets, but they were not very successful at courting. However, "non-singing males can engage in alternative reproductive strategies, such as intercepting females that approach signalling males" (Wada-Katsumata et al 2023 p1).

An example where the selection pressure is anthropogenic is the German cockroach (Blattella germanica). Females have a fondness for sugars which males exploit by producing a nuptial secretion during courtship. "A critical function of the male's nuptial gift is to arrest the female long enough for the male to extend his abdomen under the female and engage her genitalia. Short nuptial feeding by the female interrupts the genitalia grasping behaviour by the male" (Wada-Katsumata et al 2023 p2). But insecticides have been developed using sugars. However, some cockroaches have evolved an aversion to sugars (glucose-aversion mutation; GA), but they have less mating success with "traditional" cockroaches.

The situation is this: GAs females reject the nuptial gift and interrupt copulation. But GA males were found to initiate copulation faster (2.2 vs 3.3 seconds) in experiments by Wada-Katsumata et al (2023). Also the content of the nuptial gift appeared to be changing (Wada-Katsumata et al 2023).

Wada-Katsumata et al (2023) described the possible process: "As selection pressure persists, GA females would prefer GA males that express the new adaptive courtship traits (positive-assortative mating under sexual selection), biasing male-male intra-sexual contests in favour of GA males, and ultimately driving the population to homozygosity of both GA and the alternative male courtship traits. These genotypes would then be favoured because they restore both foraging and mating success and overall fitness to both sexes" (pp8-9).

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5. REPRODUCTION-RELATED BEHAVIOURS

5.1. MATE GUARDING TOAD

"Mate-guarding" involves monopolising a breeding partner for the reproductive period to stop access to other potential mates. It can occur before and/or after mating. It is a more common behaviour in males. "Mate guarding can increase the reproductive success of the monopolising individual if the cost of guarding is lower than the benefits" (Rueda-Solano et al 2022 p127).

Among anuran amphibians (frogs and toads), mate guarding is usually males performing prolonged amplexus (ie: continuing to grasp the female after mating) (for a few hours, or a night, or in extremes, weeks or months) (Rueda-Solano et al 2022) (figure 5.1).

"Mate guarding in the form of prolonged amplexus may have evolved in response to male-male scramble competition in species where the breeding season is short and the male has a fair probability of resisting removal by females and by rival amplectant males... In such circumstances, being the first male to amplect with a female would be tremendously advantageous, and hence, intra-sexual selection might lead to males initiating amplexus ever earlier, even to the point where the female is not yet ready for reproduction" (Rueda-Solano et al 2022 p128). Scramble competition is simply males attempting to breed with as many females as possible in a limited time period. It is a characteristic of "explosive breeders", which have a very limited reproductive opportunity (eg: one night), as opposed to "prolonged breeders" with a window of weeks or months. In this case, males tend to advertise their quality by calling, say (Rueda-Solano et al 2022).

The male Santa Marta harlequin toad (Atelopus laetissimus) can perform amplexus for more than a month. Rueda-Solano et al (2022) studied this species in a mountain range in northern Colombia in 2018 and 2019. Individuals were measured and the clasp force was

(Source: Bernie Kohl; public domain)

Figure 5.1 - Amplexus in common toad pair.

estimated. On average, females are larger and heavier than males, but males have developed forelimbs to aid in clasping.

Controlled observations were made, and thirty-eight displacement experiments were performed, where two different males were placed with a female.

Mated males had higher forearm width than unmated ones. The average clasp force was 18 N (equivalent to fifty times its body weight) (Rueda-Solano et al 2022).

Successful displacement of a male occurred when the unmated male was much larger than the clasping individual (the quickest removal took five hours). When the two males were of similar body size, the displacement process lasted longer (96 hours at the most in observations). Smaller males failed to displace larger males, though displacement was very low generally (seen in eight of the experiments). Rueda-Solano et al (2022) described their observations in the experiments: "During the displacement experiments, we observed that unmated males that tried to remove the amplectant male from the female's dorsum produced advertisement calls when they stood in front of the amplectant pair; they also made some visual signalling with forelimbs and hindlimbs. Both the male and female in amplexus jointly exhibited defensive behaviour against unmated intruder males. Clasped females kicked unmated males when they approached. The harassment behaviour by unmated males was continuous during the entire experiment" (p135).

Controlled observations of five pairs found that amplexus lasted on average 43 days, and males lost up to one-fifth of body weight, though this was recovered in around one week. The researchers estimated that amplexus could last between 75 and 135 days in the wild.

Males have evolved traits to limit amplexus displacement. "Under natural conditions, larger male A. laetissimus with larger forearms have up to four times more chances of being in amplexus than smaller males" (Rueda-Solano et al 2022 p136). The ability to survive without food for long periods (and recover body weight quickly) have also evolved.

Thus, an intra-sexual strategy has evolved for males to clasp a female even before she is ready to breed.

5.1. Nuptial Pad

Amplexus males have higher levels of plasma androgen levels than lone males. Androgen levels also influence the development and maintenance of "nuptial pads" or "breeding glands" (spiked swellings on the forearm which can aid in grip during amplexus). The size and darker colour of the pads is linked to male mating success (Orton et al 2023).

Orton et al (2023) studied breeding by the common frog (Rana temporaria) at sites in England (Devon) and Scotland in 2015, 2020 and 2021. The nuptial pad length was measured and photographed for male frogs caught in amplectant pairs and alone. The caught frogs were then used in an experiment where two females had a choice of eight males.

The winning males in the experiments had larger and darker nuptial pads than losers in both countries. "In total, 91% of male winning in amplexus possessed either a longer or a darker nuptial pad (or both) in frogs sampled from Devon and 89% of winning frogs possessed either a longer or a darker nuptial pad (or both) in frogs sampled from Scotland" (Orton et al 2023 p236).

This finding is important because it shows choice (or a non-random mating strategy). Common frogs are viewed as explosive breeders with a limited breeding period of 10-14 days, and so it was assumed that a random mating strategy was used (ie: mate with as many as possible in the restricted time and not worry about quality - a "scramble competition" strategy).

The researchers were not able to distinguish whether females choosing males, or the most competitive males were succeeding with their experimental design (Orton et al 2023).

5.2. PANDA CUB REJECTION

Artificial insemination (Ain) allows for a female to become pregnant and deliver offspring without a "natural mating event". This is known as "nescient mating" (Li et al 2022). But this does not include cues about quality of the male that a female uses. According to the "differential allocation hypothesis" (Burley 1986), "female perception of male differences in phenotypic quality during mating can lead to the adjustment of maternal investment in pre- and post-natal periods" (Li et al 2022 p1). Put simply, a female will invest more resources in offspring from a higher quality male.

In the case of the giant panda (Ailuropoda melanoleuca), the offspring need "near-constant body contact with the mother for thermoregulation, nursing, and genital stimulation (ie: via licking) for urination and defaecation, and therefore cub survival depends on the amount and quality of the care given by the mother" (Li et al 2022 p2). Cub rejection is the extreme of no maternal investment, and this does occur as mother give birth to twins typically in the wild (Li et al 2022).

Li et al (2022) reported data on Ain and cub rejection in China. Data were available from two research centre sites covering 1996 to 2008, and 2009 to 2018 (n = 202 cubs born to fifty-seven females). Both natural mating Ain were used over the years. In the former case, females were offered two males to choose from.

Mothers rejected 40% of cubs produced by Ain compared to 29% from natural mating. Rejection was classified based on observations of the mother-cub interactions in the first month of life. Li et al (2022) noted that their findings were "the first indication that the use of artificial insemination as a conservation breeding tool may have consequences that compromise maternal investment in offspring care" (p4).

The researchers were limited in their ability to control confounders, like prior mating experiences, and the stress of Ain. Li et al (2022) noted that an ideal experiment would have a control group who underwent a placebo Ain op (ie: no sperm injection) and then mated naturally.

5.3. POLAR BEAR INBREEDING RISK

Long-term data can help in understanding the impact of climate change on different species. One example of this is with the polar bears inhabiting the Svalbard Archipelago in the north-west Barents Sea, since 1995 (Maduna et al 2021). This area has seen an estimated 41 extra ice-free days per decade between 1979 and 2014 (Stern and Laidre 2016). This has meant "a documented northward shift in the distribution of optimal habitat for polar bears in all seasons. Coinciding with this period of sea ice loss, studies in Svalbard have revealed both reduced numbers of pregnant females reaching traditional denning areas than before and that polar bears spent less time at glacier fronts hunting seals and more time on land and near bird colonies, eating birds and bird eggs, than they did in earlier years" (Maduna et al 2021 p2).

The Barents Sea sub-population of polar bears was estimated at 2650 in August 2004 (Aars et al 2009).

The data collected since 1995 includes tissue samples, which allowed genetic fingerprinting of over 600 individuals. Over approximately 20 years, a loss of genetic diversity was found, which "may reduce the fitness of individuals and cause an elevated risk of extinction" (Maduna et al 2021 p6). Simulations of future sea ice loss suggested that it "will lead to the continued erosion of local genetic diversity in polar bears of the Svalbard Archipelago and to increased isolation between local areas, especially if there is a concurrent decrease in the number of bears" (Maduna et al 2021 p6).

Polar bears move across sea ice and mix, but open water acts as a barrier to such migration and dispersal. Less movement increases inbreeding risk (Maduna et al 2021).

5.4. OCTOPUS SELF-DESTRUCTION

Wodinsky (1977) described female octopuses as having a "'self-destruct' system", as the secretions of the "optic glands are responsible for the series of post-mating behavioural changes that lead to death. Removal of the optic glands causes female octopuses to abandon their eggs, resume feeding, and possibly mate again: in all, living for over 4 months longer than their intact counterparts" (Wang et al 2022 p2572) [10].

Usually, after mating, females brood their eggs steadfastly, while fasting, which contributes to the physiological decline, eventually to death. There is also evidence of self-injury (Wang et al 2022). The Californian two-spot octopus (Octopus bimaculoides) is an example here.

5.5. POST-COPULATORY BEHAVIOUR AND FRUIT FLIES

Post-copulatory behaviours are those that occur after copulation as part of sexual selection. For example, female fruit flies can store sperm rather than immediately fertilise eggs, and this gives them the opportunity to mate with multiple males and choose the "best" sperm. Some flies may be able to store up to four different male's sperm. There may be short-term and long-term storage organs in some flies (Perez-Staples and Abraham 2023). "By differentially string sperm, females can potentially bias paternity through cryptic choice" (Perez-Staples and Abraham 2023 p93). "Sperm mixing" is also a possibility (Perez-Staples and Abraham 2023).

This is the case when mating with different males (polyandry), but in some species the same male remates (multiple matings). "For example, in Campiglossa genalis, the male remains mounted on the female and repeats matings from two to seven times in a single event; in contrast, in Dioxyna sororcula [Blackjack fly], while there are three to four matings with the same male per mating episode, females lay one to two eggs in between matings" (Perez-Staples and Abraham 2023 p96).

On the male side, the seminal fluid may include substances that inhibit female remating. For example, molecules that reduce female sexual receptivity or the olfactory response to male sexual pheromones (Perez-Staples and Abraham 2023).

5.6. FEMALE INSECT GENITALIA

Male genitalia and associated structures ("secondary genitalia") (eg: grasping devices that coerce copulation or prevent the female from remating) are driven by sexual selection, typically female choice.

[10] The optic glands are the equivalent of the vertebrate pituitary gland (Wang et al 2022).

Female genitalia co-evolve in response (eg: ways to choose high quality sperm if copulations forced) (Browne and Gwynne 2022).

Where females depend on male investment, like nuptial gifts, there will be sexual selection pressures on females to attract males. So, now male choice will influence the evolution of female genitalia (eg: ways to stimulate males to invest or coerce into providing nuptial gifts). For example, in Australian Kawanaphila katydids the male's genitalia are grasped encouraging longer duration of copulation and a larger spermatophylax gift (ie: a nutritional supplement to sperm) (Browne and Gwynne 2022).

While the New Zealand "short-tailed" ground weta (Hemiandrus pallitarsis) (figure 5.2), which has an abdominal "device" (ie: accessory organ) to grasp the males and force them to provide the nutritious gift (separate to the sperm capsule). This is important because the female cares for the eggs and newly-hatched offspring in an underground chamber for 5-6 months without eating (Browne and Gwynne 2022).

Copulation fails when this "device" is experimentally removed (Gwynne 2005).

Females with longer accessory organs have a greater number of eggs that develop to the nymphal stage, and males have bee seen to reject females with shorter organs (Browne and Gwynne 2022).

(Source: Rudolph89; public domain)

Figure 5.2 - Short-tailed ground weta.

5.7. REFERENCES

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