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Some Research on Animal Behaviours

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

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1. TINY ORGANISMS IN THE OCEAN

1.1. BIG ANIMALS HUNT TINY PREY

"Perhaps because nature loves a paradox" (Wong 2023 p22), humpback whales (Megaptera novaeangliae) (the largest creature on earth) eat the smallest prey in the sea (krill). Several thousand pounds of these shrimp-like crustaceans are filtered out of thousands of gallons of seawater per day during feeding.

How do these whales find the swarms of krill? Toothed whales (eg: sperm whales, dolphins) use ultra-sonic sonar signals, but not baleen whales (which includes humpback whales) (Wong 2023).

One possibility is the release of chemical signals in the water ("odour landscapes"; Owen et al 2021). It is known that phytoplankton release a chemical called dimethyl sulfide (DMS) when eaten by zooplankton, which attracts seabirds like albatrosses who eat zooplankton (eg: Nevitt et al 1995) (as well as fish, turtles, and marine mammals; Owen et al 2021). Krill eat phytoplankton, so whales could also be attracted by DMS in the water (Wong 2023).

To test this idea requires measuring DMS concentrations in the ocean. Higher levels of DMS in water samples have been found where there are higher concentrations of zooplankton (Wong 2023). Baleen whales seem to congregate in such areas (eg: Owen et al 2021), which would support the hypothesis of DMS as a chemical signal detected by them. Owen et al (2021) sampled DMS in sea water over five days in June 2019 around Cape Cod, Massachusetts, USA. DMS levels positively correlated with zooplankton biomass in the area (though there was some variation). Subsequent computer simulations by these researchers showed that "following gradients of DMS would lead zooplankton predators to areas of higher prey biomass than swimming randomly" (Owen et al 2021 p1).

Recent analysis of the diets of Southern Ocean humpback whales has found a wider range of foods consumed that traditionally believed (eg: up to 60% fish; Bury et al 2024). These whales had been viewed more specialist than the generalist humpbacks in the northern hemisphere.

The main methods for tracking and studying whales include observation and photo-identification, satellite tagging, and genetic analysis. "More recently, stable isotope analysis [eg: nitrogen] has emerged as a powerful tool to investigate the trophic ecology and foraging ranges of humpback whales by analysing the stable isotope values of their tissues and prey within their foraging environments... The isotopic composition of phytoplankton at the base of the food chain (the isotopic baseline) is transferred to higher trophic levels with relatively predictable relationships" (Bury et al 2024 p124).

Bury et al (2024) used this method on whales in Antarctica (in particular, around the Balleny Islands and in the Ross Sea). Tissue samples for isotope analysis from 65 humpbacks was collected.

1.2. DIEL VERTICAL MIGRATION

The term "diel vertical migration" (DVM) describes the daily aquatic movement of an estimated ten billion tons of animals from more than 3000 feet down to the sea surface [1]. The majority of the DVM is zooplankton surfacing to feed on phytoplankton. The DVM includes temperate change (20 °F difference over 1000 feet travelled) and pressure change (table 1.1) (Courage 2022).

The pattern of migration is influenced by the light-dark change as in day to night generally, but also variations like solar eclipses, prolonged periods of dark and light as at the poles, and cloudy skies, as well as chemicals produced by fish, and internal circadian rhythms (Omand et al 2021). Omand et al (2021) found that changes in light due to cloud shadows was a trigger to some DVM in a study in the sub-arctic north-eastern Pacific Ocean. Up to one-third of distance travelled during a round-trip DVM was linked to light modulation by clouds.

The use of autonomous underwater vehicles (AUV) with cameras and other equipment has provided, in recent years, more information about the DVM. For example, "scattering layers" is a term used to describe how the different invertebrate and vertebrate species group together in midwater. The term originates from the appearance of sonar signals (Benoit-Bird et al 2017).

Benoit-Bird et al (2017) used an advanced AUV to

[1] The DVM has been called the "largest net animal movement on earth" (Hays 2003 quoted in Benoit-Bird et al 2017), and was first described over 200 years ago (Omand et al 2021).

collect data up to 600 m down in the Catalina Basin, California, over ten days and nights in September 2013. Acoustic data from an echosounder system were collected at different pulses and frequencies. The findings were presented as "the first measures of the internal layer structure, demonstrating that these features are made up of many topologically scaled, mono-specific aggregations, or 'schools' rather than an indiscriminate mix of sizes and species. Schools responded to predators using behaviour much like flash compression while neighbouring aggregations increased their spacing to maintain coherent layers. Rather than simply an incidental outcome, the formation of layers of life in the sea is a highly organised process driven, at least in part, by biotic pressures for cohesion with broad adaptive significance for the myriad species that inhabit these ubiquitous features" (Benoit-Bird et al 2017 p2788). The shallowest layer was dominated by larval fish and small crustaceans, and the lower layers by krill.

ZONE	DEPTH	ATMOSPHERE PRESSURE (atm)
Epipelagic (sunlight zone)	0-200 m	1 atm
Mesopelagic (twilight zone)	200-1000 m	
Bathypelagic (midnight zone)	1000-4000 m	200 atm at at 2000 m 400 atm at 4000 m
Abyssal	below 4000 m	600 atm at 6000 m
Seafloor		

(Source: Fischelli et al 2022)

Table 1.1 - "Ocean zones".

The phytoplankton (prey) have also been observed to move, but in the opposite direction to the zooplankton (predators). Bollens et al (2012) showed this "reverse DVM" in an experiment with planktonic dinoflagellates (single cell organisms) that reside near the surface during the day and migrate downwards at night. The experiment involved two-metre tall vertical tanks, controlled lighting conditions, dinoflagellate Akashiwo sanguinea (prey), and copepods (small crustaceans) (predators). The reverse DVM "occurred both in the absence and the presence of copepod predators, but the amplitude of the migration was greater (ie: enhanced) in

the presence of the copepods" (Bollens et al 2012 p51). For example, the prey dropped from an average depth of approximately 90 cm at midday to 100 cm at midnight when predators absent, but to 110 cm when predators present. The predators' average depth was 120 cm at midday and 70 cm at midnight.

1.3. CLIMATE CHANGE

The term "jellification" of the ocean describes the increase in numbers or biomass of jellyfish and other gelatinous zooplankton. "This perception of an ocean 'jellification' is based on a growing number of records of negative impacts of jellyfish aggregations on human enterprises, including fisheries (eg: net clogging, gear damage, reduced catch), tourism (stinging jellyfish), and clogging of water-intakes of power production systems" (Pantiukhin et al 2024 p1316).

Climate change is expected to push species polewards, and Pantiukhin et al (2024) investigated the case of gelatinous zooplankton in the Arctic Ocean. Data were taken from four open source databases for eight species (eg: Arctic comb jelly or sea nut; lion's mane jellyfish) covering 1950 to 2014, and then modelled for 2050 to 2099. Seven of the species were predicted to shift to northern latitudes, and, the researchers argued, "profound impacts on the Arctic marine environment and associated ecosystem services can be expected" (Pantiukhin et al 2024 p1316).

Chaabane et al (2024) began: "Ongoing anthropogenic carbon dioxide (CO2) emissions are warming and acidifying the ocean, leading to water-column stratification and altering ecological niches. These effects are particularly severe for organisms producing a calcium carbonate shell or skeleton because acidification impedes calcification faster than warming favours it. Furthermore, the increasing remineralisation of organic matter in the upper water column, in response to ocean warming, could alter the availability of nutrients" (p390). Planktonic foraminifera (PF) are calcifying micro-organisms who are and will be impacted.

Chaabane et al (2024) analysed data on PF since the 1910s using the FORCIS (Foraminifera Response to Climatic Stress) database. The database includes nearly 200 000 ocean water samples and their contents (Chaabane et al 2023).

Overall, PF abundance have decreased by about one-quarter in the study period, while there is evidence of

poleward migration, and some species descending in the water column. The researchers voiced concerns that the movements "will not be enough to ensure survival" (p390) as PF are highly sensitive environmental changes (Chaabane et al 2024).

1.4. REFERENCES

Benoit-Bird, K.J et al (2017) Prey in oceanic sound scattering layers organise to get a little help from their friends Limnology and Oceanography 62, 2788-2798

Bollens, S et al (2012) Predator-enhanced diel vertical migration in a planktonic dinoflagellate Marine Ecology Progress Series 447, 49-54

Bury, S et al (2024) Southern Ocean humpback whale trophic ecology, I. Combining multiple stable isotope methods elucidates diet, trophic position and foraging areas Marine Ecology Progress Series 734, 123-155

Chaabane, S et al (2023) The FORCIS database: A global census of planktonic foraminifera from ocean waters Scientific Data 10, 1, article 354

Chaabane, S et al (2024) Migrating is not enough for modern planktonic foraminifera in a changing ocean Nature 636, 390-396

Courage, K.H (2022) Stealth migrations Scientific American August, 44-49

Fischelli, M et al (2022) Dynamic seas Scientific American August, 61-63

Hays, G.C (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. In Jones, M.B et al (eds) Migrations and Dispersal of Marine Organisms Springer: Netherlands

Nevitt, G.A et al (1995) Dimethyl sulphide as a foraging cue for Antarctic Procellariform seabirds Nature 376, 680-682

Omand, M.M et al (2021) Cloud shadows drive vertical migrations of deep-dwelling marine life Proceedings of the National Academy of Sciences, USA 118, 32, e2022977118

Owen, K et al (2021) Natural dimenthyl sulfide gradients would lead marine predators to higher prey biomass Communications Biology 4, 1, article 149

Pantiukhin, D et al (2024) Pan-Arctic distribution modelling reveals climate-change-driven poleward shifts of major gelatinous zooplankton species Limnology and Oceanography 69, 1316-1334

Wong, K (2023) Big little mystery Scientific American April, 22-31

2. PETS

2.1. DOMESTIC CATS ATTACHED TO HUMANS

Dogs are much more expressive of their attachment to humans, whereas cats appear aloof and indifferent towards people (Marshall 2023). But research has shown that cats are attached to humans more subtly. This has been seen in these three study areas.

2.1.1. Socio-Spatial Cognition

"Mental representations about the whereabouts of living things such as other group members, predators, or prey are likely to be advantageous for many animals, especially in conditions of poor visibility. Noe and Laporte [2014] called this ability 'socio-spatial cognition'; it can be seen as a valuable cognitive ability that involves spatially mapping others by using auditory information such as vocalisations or other auditory cues" (Takagi et al 2021). Domestic cats (Felis catus) have "remarkable hearing ability", and research has shown the use of this ability (table 2.1) (Takagi et al 2021).

STUDY	MAIN FINDING
Takagi et al (2016)	Inference of presence of unseen inanimate objects based on hearing sounds
Takagi et al (2019)	Expecting to see owner's face upon hearing owner's voice
Takagi et al (2021)	Mapping the spatial position position of owner from voice

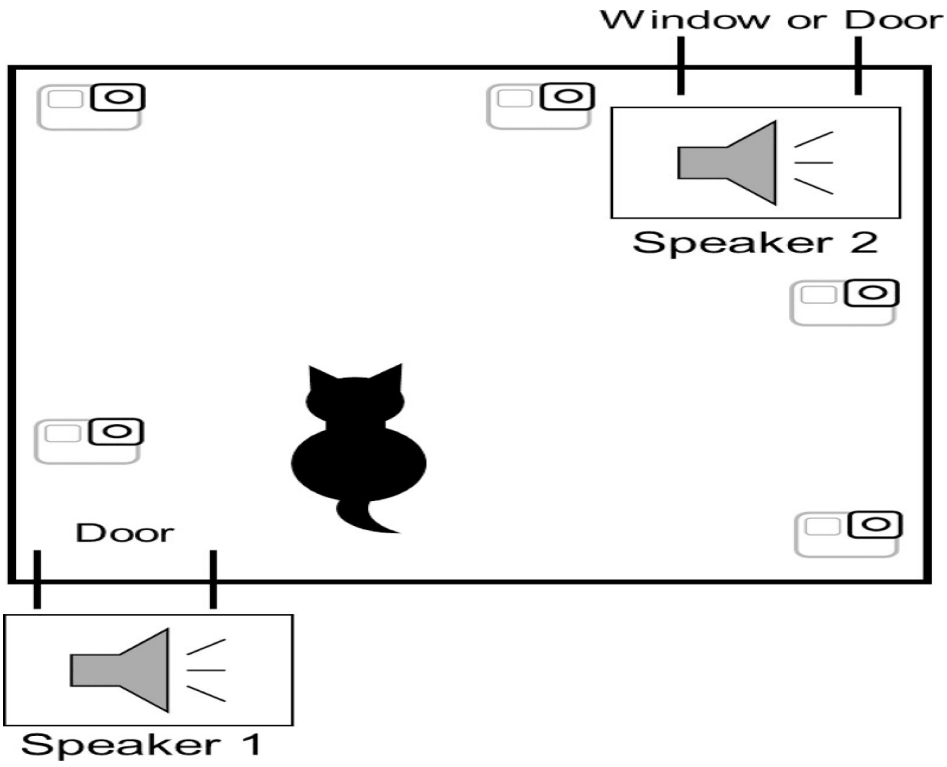
Table 2.1 - Three studies by Takagi et al showing the use of auditory information by cats.

Takegi et al (2021) used a "teleportation"-like

scenario in three experiments, which had been previously employed with vervet monkeys (Noe and Laporte 2014), for example. Two speakers were placed a distance of approximately four metres apart in a room, and sounds were played from one or both speakers sequentially (figure 2.1; table 2.2). The studies took place in an environment familiar to the cats in Kyoto, Japan. In total, 142 cats were studied.

- 1. Same sound/same location - sound A from speaker 1 followed by sound A from speaker 1
- 2. Different sound/same location - sound A from speaker 1 followed by sound B from speaker 1
- 3. Same sound/different location - sound A from speaker 1 followed by sound A from speaker 2
- 4. Different sound/different location - sound A from speaker 1 followed by sound B from speaker 2

Table 2.2 - Four conditions of the experiments.

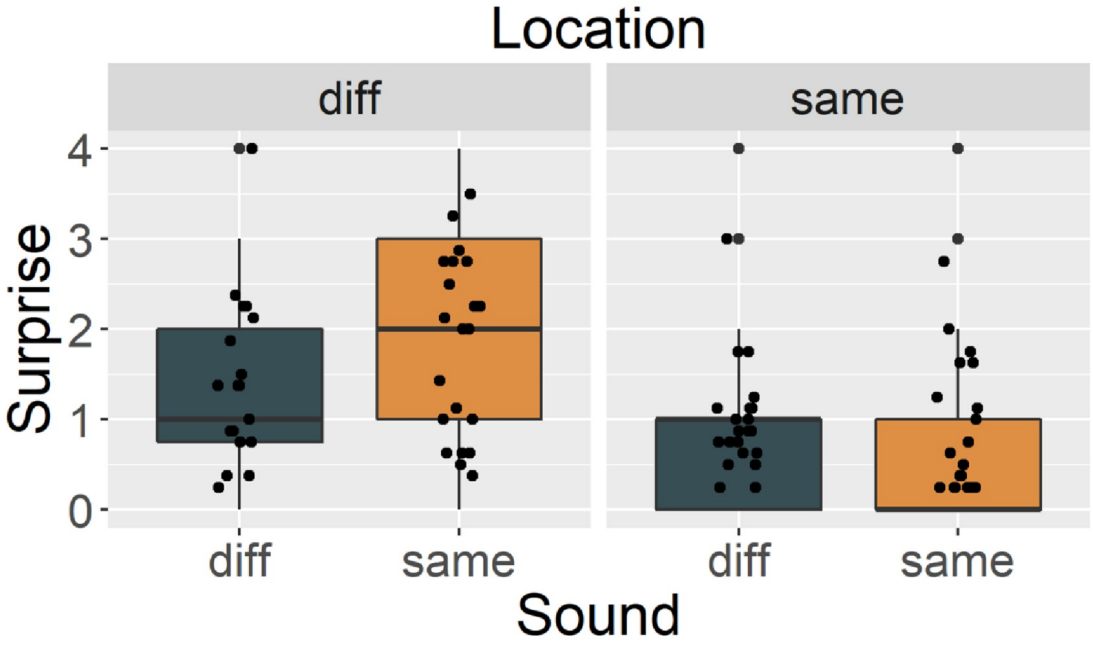


(Source: Takegi et al 2021 figure 1)

Figure 2.1 - Arrangement of the experiment.

In Experimenter 1, the owner calling the cat's name was the sound, and a stranger's voice as a control. "Surprise" (measured by behaviours like moving ears, head direction, and looking back) was the outcome measure. This was scored by eight raters from video recordings on a five-point scale (0 (no surprise) to 4 (strongly surprised)).

The cats showed more surprise when the owner's voice was played sequentially from the two different locations (ie: with 2.5 seconds between) (same sound/different location) than the same voice from the same location (figure 2.2).

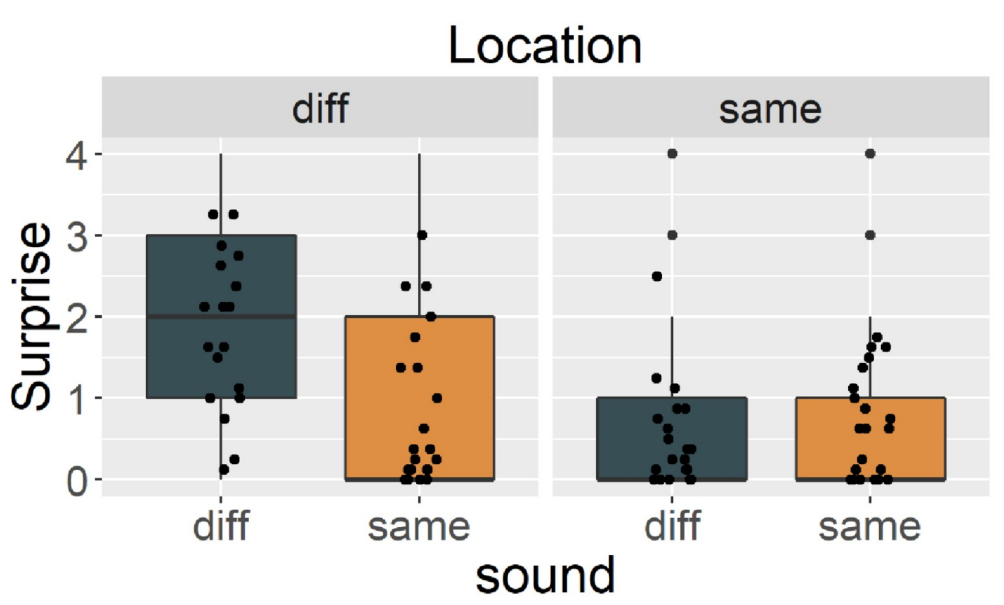


(Each dot is an individual cat's mean score)

(Source: Takegi et al 2021 figure 2)

Figure 2.2 - Scoring of surprise by eight raters in Experiment 1.

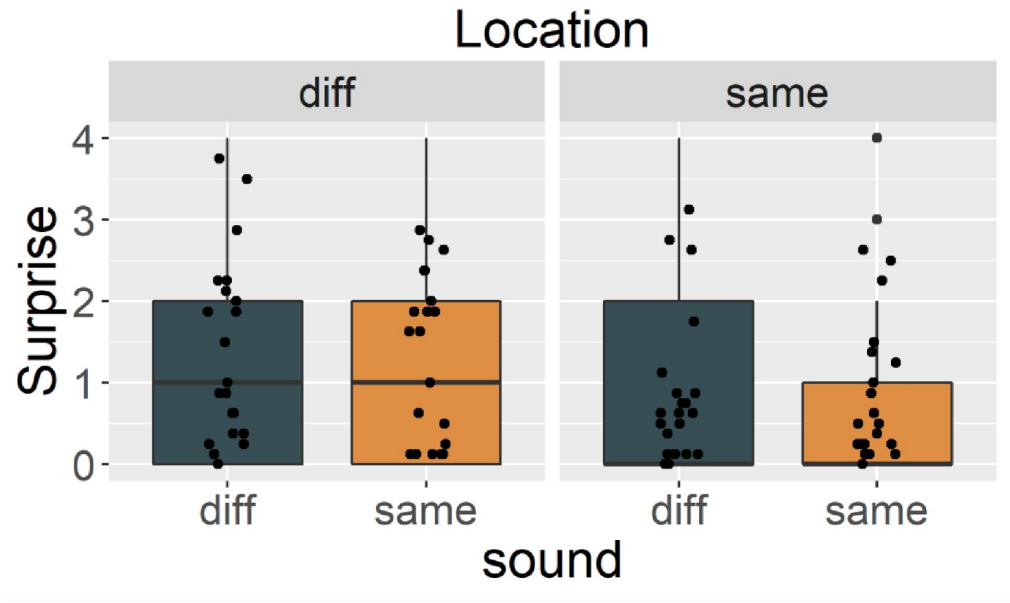
Experiments 2 and 3 used the same method, but different sounds - vocalisation of a familiar cat (Experiment 2), and non-social physical sounds (eg: door opening) (Experiment 3). In both cases the cats showed little surprise in the same sound/different location condition (figures 2.3 and 2.4). In fact in Experiment 2 the most surprise was shown in the different sound/different location condition.



(Each dot is an individual cat's mean score)

(Source: Takegi et al 2021 figure 4)

Figure 2.3 - Scoring of surprise by eight raters in Experiment 2.



(Each dot is an individual cat's mean score)

(Source: Takegi et al 2021 figure 5)

Figure 2.4 - Scoring of surprise by eight raters in Experiment 3.

The researchers summed up: "Our results suggest that cats have mental representations about their out-of-sight owner linked to hearing the owner's voice, indicating a previously unidentified socio-spatial cognitive ability" (Takagi et al 2021 p1). Such an ability would fit with an attachment bond (ie: awareness of position of attachment object).

In the research with vervet monkeys (Noe and Laporte 2014), the monkeys responded more to the calls of group members in the same sound/different location condition than the same sound/same location condition.

2.1.2. Preference for Human Interaction

Vitale Shreve et al (2017) offered 25 adult pet and 25 adult shelter cats in Oregon, USA, a choice of human social interaction, food, toys, or scent (eg: catnip), and the time spent interacting with each was measured in a three-minute session. Each category was also tested with options - for example, human vocalisation or petting; chicken or tuna.

Overall, social interactions with humans was most preferred, followed by food, for both sets of cats, though there were some individual differences.

2.1.3. Attachment Style

Vitale et al (2019) showed that cats display attachment styles towards human caregivers using the "Secure Base Test" (SBT) [2]. "During this test, the subject spends 2 minutes in a novel room with their caregiver, followed by a 2-minute alone phase, and then a 2-minute reunion phase" (Vitale et al 2019 pR864).

The reaction of the cat to the caregiver's return is the key outcome measure. "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)" (Vitale et al 2019 pR864).

Of 70 kittens (3-8 months old) tested in the Oregon

[2] The SBT was developed from the "Strange Situation Test" of attachment in human infants.

area of the USA, 64% were classified as "secure attachment", and the remainder as "insecure attachment" (mostly "ambivalent attachment"). A similar classification pattern was found with 38 adult cats in the SBT (Vitale et al 2019).

Studies with dogs and the SBT (eg: Wanser and Udell 2018) found 58% secure and 42% insecure attachment.

2.2. VEGETARIAN PETS

Owners/guardians/caregivers of cats and dogs, who often are themselves vegetarian or vegan, are exploring such diets for their pets. Andrew Knight commented: "There's a revolution under way in this sector [pet foods], driven by consumers and the concerns that they have over climate change and the health and well-being of their cats and dogs" (quoted in Lawton 2022). What is the evidence around vegetarian pet diets?

In terms of evolution, domestic cats and dogs come from carnivorous species (wolves and big cats respectively), though dogs have become more omnivorous with domestication. Cats, in particular, need certain nutrients only found in meat (eg: taurine (amino acid); arachidonic acid) (Lawton 2022).

Plant-based diets can be supplemented with necessary nutrients. Andrew Knight noted: "No species has any particular need for meat, or any other particular ingredient. What they have requirements for is a set of nutrients in a formulation that's sufficiently digestible and palatable" (quoted in Lawton 2022). While Knight (2023) commented on vegan diets in particular that "provided such diets are formulated to be nutritionally-sound, as modern commercial vegan diets usually are, dogs and cats maintained on vegan diets can have longevity and health at least equivalent, and in some respects superior, to those maintained on conventional meat-based diets. Such results are evident within studies of health outcomes in both dogs (nine studies) and cats (four studies). Dietary palatability also appears equivalent overall" (p2).

The health outcomes of pets on vegan diets has been studied by owner-reported surveys mostly. For example, Semp (2014 quoted in Knight et al 2023) surveyed owners of dogs (n = 174) and cats (n = 59) in Austria, Germany and Switzerland in 2014. "Thirty-eight of these cat and dog guardians reported healthier and shinier coats after transitioning to vegan diets. Some showed resolution of

dermatological problems. Sixteen guardians described improved odours of their pets. Some also noted increased stool volumes and improvement of stool consistency" (Knight et al 2023 p2).

Dodd et al (2021) surveyed cat owners in North America, recruited via email and postcards to customers of pet food retailers, and related social media advertisements in 2018-2019. A total of 1325 questionnaires were completed. There were 52 questions (36 multiple-choice, eight short answer, seven Likert scale, and one ranking question). Overall, 18% of cats were fed on plant-based diets only. These owners/ guardians had "a positive perception of their cats' health, and reported a belief of better general health, better body condition, and fewer health disorders as compared to owners who fed their cats MB [meat-based] diets" (Dodd et al 2021 p12). No difference in reported lifespan between the different diets. Table 2.3 lists key limitations with this study.

- 1. Self-selection - "It is likely", Dodd et al (2021) admitted that "pet owners with exceptional interest in pet health and wellness would be most likely to voluntarily participate in the study" (p11).

The researchers explained the possible consequence that "pet owners with specific interest in their pet's health and wellness may be highly perceptive and aware of conditions affecting their pet, resulting in their pet being presented to their veterinarian more often. This could either prevent health disorders by implementing appropriate prevention strategies or result in earlier diagnoses. These two potential outcomes would have opposing effects on the number of health disorders reported as prevention would decrease the number of heath disorders occurring while timely diagnosis could increase the number of health disorders reported. By collecting health data reported by cat owners and not health professionals, objective evaluation of cat
health could not be performed" (Dodd et al 2021 p11).

There was also the possibility of oversampling of pet owners with interest in unconventional diets. Many pet owners buy pet foods at supermarkets and grocery stores, and the survey was advertised at these places.

- 2. Categorisation of diets - "Of the cats fed a PB [plant-based] diet, 35% (65/187) were reported unlimited access to the outdoors, suggesting their diet could be supplemented with hunted prey to some degree" (Dodd et al 2021 p2).

- 3. General online survey issues - eg: excludes owners with no online access; reported data depends on the accuracy of recall of the owners.

- 4. Overall, the researchers accepted that the findings "represent the opinions and beliefs of cat owners, not the

definite health status of the cats, and must be interpreted as such" (Dodd et al 2021 p12). Note that veterinary practitioner surveys have advantages here, but also their own limitations (eg: owners may not take cat to vet when ill, or only when illness proves severe; depends on income to afford veterinary services).

Table 2.3 - Key limitations with Dodd et al (2021).

Knight et al (2023) reported a large-scale online survey mostly in the UK in late 2020 that covered seven general indicators of illness/disease/disorders. Analysis of the data included controlling for cat's age, sex, and neutering status, which can all affect health status. In total, 1418 cat guardians/owners participated, of which 9% had fed a vegan diet in the last year. The average cat on a vegan diet had reduced veterinarian visits and assessments as unwell, and guardian-reported disorders than meat-fed cats (table 2.4). The differences were not statistically significant. However, Knight et al (2023) concluded that "cats fed vegan diets tended to be healthier than cats fed meat-based diets" (p1).

Illness indicators (7)	Occurrence in average meat-based cat	Occurrence in average vegan cat	Relative reduction with vegan diet
Increased veterinary visits	30.9%	28.7%	7.3%
Medication use	28.2%	24.0%	14.9%
Progression onto therapeutic diet	7.1%	3.2%	54.7%
Reported veterinary assessment of being unwell	46.1%	44.5%	3.6%
Reported veterinary assessment of more severe illness	23.7%	21.9%	7.6%
Guardian opinion of more severe illness	19.9%	15.3%	22.8%
No. of health disorders per unwell cat	1.650	1.394	15.5%

https://doi.org/10.1371/journal.pone.0284132.t005

(Source: Knight et al 2023 table 5)

Table 2.4 - Prevalence of seven general indicators of illness in cats.

This survey also included 2536 dog owners/guardians. These results were published as Knight et al (2024). After controlling for age, sex, neutering status, breed size, and unusually high exercise levels in the analysis of three diet groups - dogs feed the vegan diet had the best health outcomes compared to conventional and raw meat diets.

But only main meals, not treats, table scraps or

food scrounged from elsewhere were included in the analysis (Lawton 2022).

Palatability ("how much the pet seems to 'like' its food"; Knight and Satchell 2021 p8) is important for any diet. The survey data collected by Knight and others were used here also (reported in Knight and Satchell 2021). Of dogs compared on conventional, raw meat, and vegan diets, palatability was rated as higher for raw versus conventional food, with no clear pattern for vegan diet. Ten behavioural indicators were used here - eats quickly, approaches food quickly, wags tail, jumps, vocalises, salivates, licks lips, stays near food bowl, guards food, and sniffs food. The last one was the only negative indicator.

With cats, fifteen behavioural indicators were used (table 2.5), and no difference was found in diet and palatability. Knight and Satchell (2021) concluded that "vegan pet foods are generally at least as palatable to dogs and cats as conventional meat or raw meat diets" (p1).

Positive (5)	rapid approach to food, vocalisations, eating quickly, remaining near food bowl, guarding food
Negative (4)	lick food, sniff/investigate food, drop food, leave food uneaten
Indeterminate (6)	flick ears, flick tail, lick lips, lick nose, lick bowl, groom body

https://doi.org/10.1371/journal.pone.0253292.t004

(Source: Knight and Satchell 2021 table 4)

Table 2.5 - Behavioural indicators of feline palatability used by Knight and Satchell (2021).

These researchers admitted that the behavioural indicators of feline palatability, in particular, were open to dispute. For example, "licking of nose" has been viewed as a positive sign of palatability (eg: Hanson et al 2016), but as a negative sign also (eg: Van den Bos et al 2000), while Knight and Satchell (2021) classed it as indeterminate.

While in a previous study of palatability by eight beagles, Callon et al (2017) argued that "dogs lack innate preferences for animal- or vegetable-based diets similar to those found in commercial formulas. They concluded that any apparent differences in interest levels may be due to other factors, such as level of satiety, or specific ingredients or processing techniques

employed to enhance palatability" (Knight and Satchell 2021 p18).

Concerns over the environmental impacts of dog and cat diets are not unfounded. For example, "domestic dogs have a total global biomass of around 20 million tonnes – approximately equal to the combined biomass of all remaining wild terrestrial mammals. Cats have a total biomass of around two million tonnes – almost double that of the African savanna elephant. It has been reported that pets consume about 20% of the world's meat and fish, and that an area double the size of the UK is used to produce dry pet food for cats and dogs each year. Approximately three million tonnes of fish are consumed within UK pet food annually. In the US, meat produce consumption by dogs and cats appears responsible for up to 80 million tons of methane (CH_4) and nitrous oxide (H_2O) production" (Knight 2023 p2).

With these facts in mind, Knight (2023) sought to quantify the environmental benefits of vegan diets for dogs and cats (and humans [3]). The calculation involved estimating the global population of cats and dogs and their energy requirements, the pet food ingredients and their carbon footprint (including livestock numbers required), and the difference with a move to plant-based foods. Data for the USA in 2020 and globally in 2018 were used.

"Full transition to nutritionally-sound vegan diets would spare from slaughter the following numbers of terrestrial livestock animals annually (billions): US: dogs – 1.7, cats – 0.2, humans – 7.8, and globally: dogs – 6.0, cats – 0.9, humans – 71.3, as well as billions of aquatic animals in all dietary groups. Very large impact reductions were also associated with land and water use, emissions of greenhouse gases (GHGs), acidifying and eutrophifying gases, and biocide use, in all dietary groups" (Knight 2023 p1). Assuming a global change in diet, large areas of land would thus be freed up and freshwater volumes saved. Comparisons were made with individual countries to represent the gains (table 2.6).

[3] Including reducing food waste, Frischmann et al (2022) suggested that if every human in the world adopted healthy consumption practices and a plant-rich (not necessarily vegetarian) diet, 166 million metric tons of food waste would be saved over the next thirty years. This assumes that 30-40% of food intended for human consumption is wasted, as is the current situation (Frischmann et al 2022).

BENEFITS	DOGS	CATS
Land freed up from livestock production for pet foods (equivalent size)	Saudi Arabia or Mexico	Japan or Germany
Saved freshwater volumes in pet food production (equivalent renewable freshwater)	Denmark	Jordan
Reduced GHGs (equivalent to emissions)	South Africa or the UK	Israel or New Zealand
Number of additional humans fed using food energy savings from changing pet food production (equivalent population size)	European Union	France or the UK

Table 2.6 - Equivalent benefits of vegan diets for all dogs and cats globally.

2.3. REFERENCES

Callon, M.C et al (2017) Canine food preference assessment of animal and vegetable ingredient-based diets using single-pan tests and behavioural observation Frontiers in Veterinary Science 4, article 154

Dodd, S.A.S et al (2021) A cross-sectional study of owner-reported health in Canadian and American cats fed meat- and plant-based diets BMC Veterinary Research 17, article 53

Frischmann et al (2022) More food, less waste Scientific American 31, 3, 64-71 (Special edition: Science for Social Justice)

Hanson, M et al (2016) Facial expressions and other behavioural responses to pleasant and unpleasant tastes in cats (Felis silvestris catus) Applied Animal Behaviour Science 181, 129-136

Knight, A (2023) The selective benefits for environmental sustainability of vegan diets for dogs, cats and people PLoS ONE 18, 10, e0291791 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0291791)

Knight, A & Satchell, L (2021) Vegan versus meat-based pet foods: Owner-reported palatability behaviours and implications for canine and feline welfare PLoS ONE 16, 6, e0253292 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0253292)

Knight, A et al (2023) Vegan versus meat-based cat food: Guardian-related health outcomes in 1369 cats, after controlling for feline demographic factors PLoS ONE 18, 9, e0284132 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0284132)

Knight, A et al (2024) Vegan versus meat-based dog food: Guardian-reported health outcomes in 2536 dogs, after controlling for canine demographic factors Heliyon 10, e35578

Lawton, G (2022) Meat-free mutts and moggies New Scientist 24th September, 45-48

Marshall, M (2023) The truth about cats New Scientist 11th March, 46-49

Noe, R & Laporte, M (2014) Socio-spatial cognition in vervet monkeys Animal Cognition 17, 3, 597-607

Takagi, S et al (2016) There's no ball without noise: Cats' prediction of an object from noise Animal Cognition 19, 5, 1043-1047

Takagi, S et al (2019) Cats match voice and face: Cross-modal representation of humans in cats (Felis catus) Animal Cognition 22, 5, 901-906

Takagi, S et al (2021) Socio-spatial cognition in cats: Mentally mapping owner's location from voice PLoS ONE 16, 11, e0257611 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0257611)

Van den Bos, R et al (2000) Taste reactivity patterns in domestic cats (Felis silvestris catus) Applied Animal Behaviour Science 69, 2, 149-168

Vitale, K.R et al (2019) Attachment bonds between domestic cats and humans Current Biology 29, R864-R865

Vitale Shreve, K.R et al (2017) Social interaction, food, scent or toys? A formal assessment of domestic pet and shelter cat (Felis silvestris catus) preferences Behavioural Processes 141, 3, 322-328

Wanser, S.H & Udell, M.A.R (2018) Does attachment security to a human handler influence the behaviour of dogs who engage in animal assisted activities? Applied Animal Behaviour Science 210, 88-94

3. WILDLIFE DOCUMENTARIES

3.1. A PRESENTATION OF NATURE

Wildlife documentaries have an important role to play in a world of biodiversity loss and extinction of species, and human urbanisation and so less contact with nature (eg: "extinction of experience"; Soga and Garston 2016).

But "nature documentaries have been accused of presenting a pristine view of the natural world and excluding the presence and impacts of humans..., potentially as a result of commercial pressure to provide entertainment to viewers... This is also the case for other media designed primarily for entertainment value, such as video games, which can present the natural world as more risky and dangerous than reality (eg: predators are often portrayed as aggressive towards humans, despite the contemporary risk they pose to humans being relatively low)... Moreover, the natural world is often presented in popular media through a white, colonial lens... — as a pool of resources that humans should extract from or manage, rather than existing as an environment in its own right, which can be enjoyed passively or merely observed" (Howlett et al 2023 p634).

Howlett et al (2023) analysed a sample of nature documentaries made between 1918 and mid-2021 (fifteen each from seven time periods: pre-1970, 1970s, 1980s, 1990s, 2000s, 2010s, and 2020s). Five minutes of each documentary was randomly sampled for the organism, habitat, and conservation/human impact message.

In total, there were 374 organisms in the total sample (105 documentaries), with one-third being mammals, and an over-representation generally of vertebrates. The most common habitat was tropical forest, and the least common was deep ocean. Conservation was mentioned in 16% of all documentaries, but in almost half of the 2010s and 2020s extracts. Anthropogenic impact was never mentioned before the 1970s.

The researchers concluded: "Wildlife documentaries have clear capacity for depicting a wide range of species and ecosystems, with potential to increase public awareness and appreciation of a broader range of groups

and support for conservation efforts... However, the range of species and habitats represented has not increased over time, potentially limiting the medium's ability to engage audiences with less-familiar taxa and habitats, or to increase engagement with more familiar, local, urban areas. We call for more work to identify reasons why certain taxa and habitats are under-represented and solutions to make them more attractive to documentary makers and public audiences alike" (Howlett et al 2023 p641). The term "Cinderella" mammal species, for example, has been used (183 threatened, overlooked species that could appeal to the public; Smith et al 2012).

3.2. LIVESTREAMING

Wildlife documentaries are usually edited programmes showing the "best bits" collected by film makers, but there are also live programmes ("livestreaming"), like "The Great Moose Migration" on Swedish television. von Essen and Peterson (2024) analysed this programme and the associated social media.

The programme is broadcast annually in April-May for 4-5 weeks, and episodes from 2019 to 2023 were analysed along with posts on the Facebook fan page, as well as material created in 2024 (eg: livechat on the "Duo" app).

It is an example of "event-based TV" (Kjus 2009 quoted in von Essen and Peterson 2024), like "Fat Bear Week Alaska", "Elephant Seal Homecoming Day", and "Aussie Penguin Parade" (von Essen and Peterson 2024). "Unlike continuous livefeeds such as 'Africam' [4], or national park cameras which broadcast continuously over the year, 'The Great Moose Migration' is time-limited to the spring when moose make their way – famously via swimming an icy river – to their summer pastures near the mountains for better grazing land" (von Essen and Peterson 2024 p3).

Such programmes are also examples of "Slow-TV", a genre like "watching a wood fire burning in a fireplace" (Antunes 2018 quoted in von Essen and Peterson 2024). There is further a "Reality-TV" element. "The genre is sometimes called direct cinema (filming subjects in their normal routines) or observational cinema in which the 'audience learns from observing events rather than being told what their significance is'(Bouse 1998...). In this format, the programme actively distances itself from the melodramatic editing style of blue-chip wildlife documentaries" (von Essen and Peterson 2024 p5).

[4] https://www.africam.com/.

The social media-related groups is "a 'hyper-multi-media' [Sixto-Garcia et al 2022] based sociality around TV shows" (von Essen and Peterson 2024 p4), or "participatory media". Kroon and Nilsson (2023) commented: "When viewers watch moose TV on multiple screens while also chatting in the Duo app and checking FB, skipping between cameras, looking at the map and keeping track of the moose counter, agonizing over how many swimming moose they just missed, how slow then, is slow TV, really?" (quoted in von Essen and Peterson 2024).

Previous research (Kroon and Nilsson 2023) has established that the feel of authenticity was important to viewers, "the alleged 'unfiltered', 'untouched' and 'real' qualities of the broadcast" (von Essen and Peterson 2024 p5). However, often information is withheld to avoid poaching (eg: GPS co-ordinates of collared animals).

Such programmes and the associated social media have critics. For example, writing a while before "The Great Moose Migration", Bagust (2008) observed: "The networked sovereign consumer-as-hero subject may be less interested in 'real' nature and its conservation than in the pleasure of interacting with the human and animal 'celebrities' and 'behavioural/geographical possibilities' of his/her own, fantastic 'imagineered' 'Web 2.0' virtual natures" (quoted in von Essen and Peterson 2024). von Essen and Peterson (2024 continued on: "Specifically, critics argue that many wildlife programmes, citizen science or entertainment based, can become focused around competition and gamification, turning sightings of species from meaningful encounters into currencies like badges and rewards, and hence say more about the user than their relationship to the animal" (p7).

von Essen and Peterson (2024) accepted that "The Great Moose Migration" has raised the interest in moose for the Swedish public, but it is "mediated and limited to the cloud rather than the corporeal moose. Insofar as this new way of consuming moose may be said to be emancipatory of past conventions, developments around the show and audience requests also demonstrate that viewers crave certain hallmarks and tropes of wildlife documentaries. In other words, conventions and societal forces also re-shackle wildlife representations to business-as-usual" (p9).

3.3. REFERENCES

Antunes, L.R (2018) Slow TV: The experiential and multi-sensory documentary. In Brylla, C & Kramer, M (eds) Cognitive Theory and Documentary Film Cham: Springer International Publishing

Bagust, P (2008) "Screen natures": Special effects and edutainment in "new" hybrid wildlife documentary Continuum 22, 2, 213-226

Bouse, D (1998) Are wildlife films really "nature documentaries"? Critical Studies in Media Communication 15, 116-140

Howlett, K et al (2023) Wildlife documentaries present a diverse, but biased, portrayal of the natural world People and Nature 5, 633-644

Kroon, A & Nilsson, J (2023) How slow is "slow TV"? Audiences' experiences of meditation, obsession and authenticity when watching swimming moose on Swedish television Journal of Popular Television 11, 3, 279-298

Sixto-Garcia, J et al (2022) Television debates, live tweeting and social audience. In Garcia-Orosa, G (ed) Digital Political Communication Strategies: Multi-Disciplinary Reflections Cham: Springer International Publishing

Smith, R.J et al (2012) Identifying Cinderella species: Uncovering mammals with conservation flagship appeal Conservation Letters 5, 3, 205-212

Soga, M & Garston, K (2016) Extinction of experience: The loss of human-nature interactions Frontiers in Ecology and the Environment 14, 2, 94-101

von Essen, E & Peterson, J (2024) Digital wildlife expeditions and their impact on human-wildlife relations: Inside the phenomenon of livestreaming an annual moose migration Digital Geography and Society 7, 100097

4. COGNITIVE ABILITIES

4.1. LONG-TERM SOCIAL MEMORY

"Complex sociality requires individuals to recognise and remember conspecifics across space and time. Long-term memory for social partners and interactions allows animals to build individual relationships, strategically navigate dominance hierarchies and alliances, and avoid hostile interactions. Humans are notable within the animal kingdom for our ability to remember others' names and faces and track information about social roles, groups, and relationships for decades" (Lewis et al 2023 p1).

Lewis et al (2023) investigated long-term social memory [5] with 26 captive chimpanzees and bonobos from three locations (Scotland, Japan, and Belgium). A preferential-looking eye-tracking task was used. This involved presenting two pictures simultaneously on a computer screen and the direction of the gaze of the viewer (ie: their attention) is recorded. In this case, a photograph of a previous groupmate and a stranger of the same species were presented together. A "differential looking score" (DLS) is calculated (ie: the time spent looking at a familiar photograph minus the time spent looking at an unfamiliar photograph).

Lewis et al (2023) summarised the findings thus: "Apes' attention was biased toward former groupmates, indicating long-term memory for past social partners. The strength of biases toward former groupmates was not impacted by the duration apart, and our results suggest that recognition may persist for at least 26 years beyond separation. We also found significant but weak evidence that, like humans, apes may remember the quality or content of these past relationships: apes' looking biases were stronger for individuals with whom they had more positive histories of social interaction" (p1).

The use of captive animals had the advantage that there was full information about relationships over the

[5] Also called "long-term social recognition" (LTSR) (Bruck 2013).

lifetime. In other words, it was known by the researchers who should be familiar and unfamiliar to each participant.

The research findings support an evolutionary basis to long-term social memory in a common ancestor of humans, chimpanzees and bonobos six to nine million years ago. This ability "likely provided key foundations for the emergence of uniquely human forms of interaction and co-operation, such as inter-group trade appearing at least 500 000 years ago, as our species expanded into distant environments and experienced extended periods away from familiar individuals. Long-lasting memory for groupmates, especially close social partners, thus may have aided in the stability of early humans' dyadic relationships and facilitated the evolution of cooperative cultural systems that extend across time, space, and group boundaries" (Lewis et al 2023 p6).

Multi-year social memory has also been reported in fur seals, sheep, elephants, and bottlenose dolphins, for instance (Lewis et al 2023). Most of the studies here have investigated LTSR for calls (eg: Bruck 2013; table 4.1).

- Bruck (2013) studied LTSR of signature whistles of individual bottlenose dolphins by 43 individuals housed in six breeding facilities in North America and the Caribbean. The average duration of housing together was four years, and the average length apart was six years. Individual dolphins were played a familiar and an unfamiliar whistle in a randomised order, and their response was observed (eg: approached the speaker playing the sound).

- There was a significantly higher response to familiar than unfamiliar whistles. This was true even with the longest separations (up to twenty years). "Duration of association did not affect recognition, meaning long periods of association were not required for long-term recognition. Interestingly, calves of less than 1 year are behaviourally less discriminating than adults or juveniles.... Sex (both respondent and caller) and kinship status did not affect recognition. This is expected given that both males and females inhabit socially complex groups, and both kin and non-kin would need to be remembered in networks of at least 60–70 individuals with whom they co-operatively hunt and engage in predation defence" (Bruck 2013 p4).

Table 4.1 - Bottlenose dolphins (Bruck 2013).

References

Bruck, J.N (2013) Decades-long social memory in bottlenose

dolphins Proceedings of the Royal Society B 280, 20131726

Lewis, L.S et al (2023) Bonobos and chimpanzees remember familiar conspecifics for decades Proceedings of the National Academy of Sciences, USA 120, 52, e2304903120

4.2. FOOD CACHING AND BRAIN ACTIVITY

The hippocampus is key to remembering information, especially for food-caching birds. "Birds remember not only the location but also the content and the relative time of a cache. By convention, these three components ('what, where, when') define a memory as 'episodic-like'" (Chettih et al 2024 p1922).

Chettih et al (2024) recorded neural (electrical) activity in the hippocampus of the black-capped chickadee. This was done by a lightweight miniature microdrive strapped to the head and a silicon probe (surgically) implanted into the anterior hippocampus of five birds.

New memories are formed when food is cached, and this was recorded in an arena with 128 possible cache sites (transparent plastic wells with a cover). Sunflower seeds were provided from motorised feeders for brief periods. Four types of behaviour were observed with video cameras - cache, retrieval, check (opening a site cover without caching or retrieving), and visits (landing at a site without opening the cover).

Brain activity during caching was different from other events, and neurons had "unusually high or low firing rates" (Chettih et al 2024 p1923). Excitatory cells were "largely silent" at this time, while a small number of cells were very active (called "cache responses"). The researchers described the pattern of neuron cells firing at this time as "barcode-like". "Each 'barcode' uniquely represented a caching event and transiently reactivated during the retrieval of that specific cache" (Chettih et al 2024 p1922).

The researchers concluded: "We propose that animals recall episodic memories by reactivating hippocampal barcodes. Similarly to computer hash codes, these patterns assign unique identifiers to different events and could be a mechanism for rapid formation and storage of many non-interfering memories" (Chettih et al 2024 p1922).

The study findings may not be generalisable to other forms of episodic memory, though they are applicable to other species, the researchers argued. Chettih et al (2024) explained: "Food caches are relatively simple

events that occur at single moments in time. Episodic memory, however, can reference multiple temporally linked events and recall them in an entire sequence.1 Neural signals in our study have also been analysed across a relatively short timescale of 1 hour, which is in the range of intermediate-term memory. Episodic memories, in contrast, are often stored long term and can last a lifetime. Even chickadees have been shown to remember caches for up to a month in spite of typically retrieving food within several hours. We do not know if barcodes are used in these more general conditions or whether they interact with other hippocampal mechanisms of episodic memory. Finally, our results do not speak to the cellular or synaptic mechanisms of memory storage" (p1932).

Reference

Chettih, S.N et al (2024) Barcoding of episodic memories in the hippocampus of a food-caching bird Cell 187, 1922-1935

4.3. TOOL USE BY BUGS

There are assassin bugs that appear to deliberately cover themselves with plant resins, such they are known as "resin bugs" or "sticky bugs". There is discussion as whether this behaviour is "tool use" (Soley and Herberstein 2023).

But what is the purpose of this behaviour? Soley and Herberstein (2023) investigated with a new species of assassin bug (Gorareduvius [6]) in Western Australia. These bugs are found on "spinifex grass", from which a sticky resin comes. Observations of 35 female and 26 male adults and 49 nymphs showed the bugs scraped the resin off leaves and "meticulously applied it over the body, particularly onto the forelegs" (Soley and Herberstein 2023 p2) [7].

Resin-equipped and resin-deprived bugs were presented with one of two prey species (flies or ants) in an experiment. In total there were 129 predation trials

[6] Subsequently named as Gorareduvius gajarrangarnang (Tatarnic et al 2024).

[7] In a separate experiment, fifteen nymphs reared in isolation showed resin-scraping and application (Soley and Herberstein 2023). The researchers commented: "Tool-users can be categorised as being either stereotyped (ie: showing 'hard-wired' behaviour) or flexible (eg: using a tool for various purposes). Gorareduvius would thus represent a case of stereotypic tool-use, because the behaviours were consistently expressed in all individuals, in the absence of training or demonstration from conspecifics, including in freshly hatched, isolated nymphs. This also seems to be the case with other assassin bugs. More generally, stereotypic tool-use appears to be the only type of tool-use that has evolved in insects" (Soley and Herberstein 2023 p3).

with twenty-six adult bugs. A repeated measures design was used.

Bugs were more successful at prey capture when resin-equipped. Resin-depleted bugs needed more attacks for prey capture, and flies, for example, had a better chance of escape after grasping by these bugs. "Spinifex resin conveyed a predatory advantage to the assassin bugs. This advantage likely derived from the resin's adhesive properties. Prey could still escape after being touched by the assassin bugs, but this was less likely to happen if the assassin bugs were equipped with resin. However, prey never appeared to be fully stuck to the resinous surface of the assassin bugs. Rather, it appears that brief, temporary adhesion, delayed prey responses sufficiently enough for the assassin bugs to grasp and stab their prey" (Soley and Herberstein 2023 p3) [8].

In relation to tool use behaviour, Soley and Herberstein (2023) made this argument: "Widely used definitions of tool-use commonly require that a tool should be detached from its environmental surrounding, and be manipulated by the animal to achieve an adaptive benefit. Our study supports that resin can be regarded as a tool used by Gorareduvius in the context of predation — the assassin bugs manipulated an environmental item (the resin), by taking it out of its usual context and applying it onto their bodies, thus gaining a selective advantage through improved prey capture. The advantage was maintained across different prey items, suggesting that this tool offers a generalised improvement in prey capture, for both flying and non-flying prey of different sizes" (p3).

References

Soley, F.G & Herberstein, M.E (2023) Assassin bugs enhance prey capture with a sticky resin Biology Letters 19, 20220608

Tatarnic, N.J et al (2024) Gorareduvius gajarrangarnang, a new species of resin-using assassin bug (Hemiptera: Reduviidae: Harpactorinae) from Australia, with notes on its behaviour Australian Journal of Taxonomy 74, 1-13

Zhang, G & Weinrauch, C (2013) Sticky predators: A comparatvie study of sticky glands in harpactorine assassin bugs (Insecta: Hemiptera: Reduviidae Acta Zoologica 94, 1, 1-10

[8] This fits with the "sticky trap predator" hypothesis (Zhang and Weinrauch 2013).

4.4. ASIAN ELEPHANTS AND WATER-HOSE TOOL USE

Two Asian elephants at Berlin Zoo were observed to use water hoses in particular ways when showering each day. Urban et al (2024) explored this interesting tool use behaviour.

1. "Mary" showed sophisticated hose-showering behaviours. She "showered her body systematically and co-ordinated the trunk-held water hose with limb movements, such as raising a hindleg and reaching forward to access it more easily with the jet of water" (Urban et al 2024 p5602).

More than that, she "adjusted the length of the distal end of the water hose according to the body part she was going to shower and showed precisely co-ordinated body movements, making sure that the water reached specific body parts. By using the water hose as an extension of her trunk, Mary improved the efficacy and reach of her showering behaviour. She adapted the tool for different purposes by changing her grip on it and, with that, its physical properties, its range, and the way she could swing it on her back" (Urban et al 2024 p5603). This is the modification of one tool for different purposes. Elephants in the wild and in captivity have been seen to use and modify branches for fly switching (Hart et al 2001).

Flexibility was observed when researchers offered three water hoses of different diameters on different days.

2. "Anchali" was involved in aggressive interactions with Mary during the latter's showering time, specifically disrupting the flow of water. Five behavioural elements were observed as shown by Anchali - hose positioning, lifting, kinking, regrasping the kink, and compressing the kink.

The researchers interpreted the behaviour as intentional for five reasons: "(1) Anchali repeatedly showed this complex sequence of trunk manoeuvres. (2) Disruptions of the water flow became more effective over time. (3) The hose had to be kinked and squeezed powerfully for disruptions to occur. (4) This occurred in close association with on-hose trunk stands. (5) There would have been a motive for Anchali to interfere with Mary's showering, as there were numerous aggressive acts by Mary toward Anchali" (Urban et al 2024 p5604).

There was a third elephant, "Pang Pha", and all

three showed individual differences in showering behaviour.

References

Hart, B.L et al (2001) Cognitive behaviour in Asian elephants: Use and modification of branches for fly switching Animal Behaviour 62, 839-847

Urban, L et al (2024) Water-hose tool use and showering behaviour by Asian elephants Current Biology 34, 23, 5602-5606

4.5. STATISTICAL INFERENCE BY CROWS

"Statistical inference, the ability to use limited information to draw conclusions about the likelihood of an event, is critical for decision-making during uncertainty" (Johnston et al 2023 p3238). Initially believed to be unique to humans, this ability has been shown in non-human primates and birds.

Here is an example of experiments with two hand-reared male carrion crows (Corvus corone) by Johnston et al (2023) that trained them to associate reward probabilities varying from 10% to 90% to nine arbitrary stimuli (eg: circle shape; triangle shape). A reward probability is the likelihood of a reward after the correct behaviour. So a 50% reward probability would mean that the crow was rewarded half the time that they correct behaviour was shown.

After training (with around 1000 trials) using a touch screen appratus, two stimuli were presented in a forced-choice paradigm in 36 conditions. Both crows chose the stimulus associated with the greater reward probability significantly more often than chance (of 50%) (ie: overall average 75%). This learning was maintained after one month. The optimal choice was varied between the left and right side to avoid association of the correct choice with one side.

The crows were more successful in the optimal choice when the distance between the probabilities was larger (eg: 90% vs 10% than 20% vs 30%).

Statistical inference can be divided into two types (Johnston et al 2023):

a) Population-to-sample - "one draws a conclusion about a sample based on population information that is either visible to the subject immediately prior to, or at the time of, decision-making" (Johnston et al 2023

p3241).

b) Sample-to-population - "one draws a conclusion about the population using sample information, which must be mentally stored and updated for each new sample. Consequently, cognitive demands are significantly higher during sample-to-population inferences and are therefore more difficult to make" (Johnston et al 2023 p3241).

The crows in the study showed the latter (Johnston et al 2023).

This study developed on one by Roberts et al (2018) with pigeons who had to learn symbols associated with two reward probabilities (25% or 75%).

References

Johnston, M et al (2023) Crows flexibly apply statistical inferences based on previous experience Current Biology 33, 3238-3243

Roberts, W.A et al (2018) Pigeons play the percentages: Computation of probability in a bird Animal Cognition 21, 575-581

5. CROCODILE ATTACKS IN TWO COUNTRIES IN SOUTH-EAST ASIA

5.1. SOLOMON ISLANDS

Saltwater crocodiles (Crocodylus porosus) attack locals and their livestock in coastal areas of the Asia-Pacific region. Collecting data on these events is important to help in developing strategies to reduce attack risks.

National and local surveys are employed. In the case of the Solomon Islands, van der Ploeg et al (2019) was an example of a national survey, while Aswani and Matanzima (2024) reported local data from four villages in the Roviana Lagoon. The former included 225 crocodile attacks on people in 234 villages between 1998 and 2017, of which 83 were fatal. The majority of victims were male.

Aswani and Matanzima (2024) collected their data in May 2023 from sixty households, and covered the period from 2000 to 2020. Interviewees in twenty households reported an encounter or an attack by a crocodile (only two attacks were fatal). The victims overall were more likely to be female.

Aswani and Matanzima (2024) noted the gender difference in victims: "All the women attacked were searching for shellfish, an activity typically undertaken by women in the Roviana Lagoon, whereas the four men were fishing. This contrasts with the national level data, which indicated that women were mostly attacked while washing clothes... Women have a significant role in gathering marine shellfish in the Roviana Lagoon, for both subsistence and sale... Recommendations for alternative livelihoods, to reduce vulnerability to crocodile attacks, could be tailored towards local women, but would need to consider regional variations in activities known to increase vulnerability to attacks. Nationally, most incidents occurred when people were fishing or diving" (pp345-346).

5.2. TIMOR-LESTE

In the case of Timor-Leste, the number of saltwater crocodile attacks has been increasing in recent years. For example, 45 attacks (82% fatal) between 2007 and 2014 in one study (Sideleau et al 2016), and 104 attacks (58% fatal) in the same period in another study (Brackhane et al 2018), which also found 26 attacks between 1998 and 2006.

Brackhane et al (2024) collected data in September/October 2022 from seven villages for the period 2015 to 2022. In both studies by Brackhane et al, the method was to ask the traditional elder and other community members about attacks, and then visit the victims (if possible). There were 46 attacks reported during 2006 and 2022 (355 fatal), of which thirty-five occurred during the focused period of 2015-2022 (34% fatal). The victims were mostly men, attacked whilst fishing or collecting mud crabs. "Use of wetlands for subsistence, particularly fishing, is critical to the well-being of local people in Timor-Leste but is the activity that most attack victims were engaged in" (Brackhane et al 2024 p349).

In their study, Sideleau et al (2016) used publicly available data through the media, local reports and official records that were placed on the "CrocBITE" database. The fatality rate was higher than in neighbouring West Timor (Indonesia) for the same period (57%) (Sideleau et al 2016). Using reported attacks misses unreported attacks, while the recall of locals as the source of information depends on accuracy of memory, and willingness to report the event to researchers (eg: individual involved in illicit activity at the time of attack may want to keep quiet).

5.3. REFERENCES

Aswani, S & Matanzima, J (2024) Human-crocodile interactions in the western Solomon Islands: The importance of local data for reducing attacks in people Oryx 58, 3, 344-346

Brackhane, S et al (2018) When conservation becomes dangerous: Human-crocodile conflict in Timor-Leste Journal of Wildlife Management 82, 1332-1344

Brackhane, S et al (2024) Wildlife conservation through traditional values: Alarming numbers of crocodile attacks reported from Timor-Leste Oryx 58, 3, 347-350

Sideleau, B.M et al (2016) An analysis of recent saltwater crocodile (Crocodylus porosus) attacks in Timor-Leste and consequences for management and conservation Maritime and Freshwater Research 68, 801-809

van der Ploeg, J et al (2019) Human-Crocodile Conflict in Solomon Islands Penang, Malaysia: WorldFish

6. PLAYFUL TEASING

Teasing (or spontaneous playful teasing) is a "cognitive precursor" of joking. Joking "draws on social intelligence, an ability to anticipate future actions and an ability to recognise and appreciate the violation of others' expectations... Like joking, playful teasing walks a fine line between aggression and play; it is mutually enjoyable, occurs in close relationships, requires the anticipation of another's response and involves creating 'unexpected' moments that deviate from expected interaction norms. Playful teasing has the potential to create mutual amusement, which may serve to maintain or strengthen social bonds" (Laumer et al 2024 p1).

The teaser must be able to understand how the recipient will respond, and the recipient must be able to distinguish the intent of the teaser. Human infants show playful teasing in three forms (Laumer et al 2024):

i) Offer and withdrawal of objects - Offer an object to another person and as they reach for it, withdraw it.

ii) Provocative non-compliance - Perform a prohibited action or refusing to perform an expected one.

iii) Disrupting others' activities - eg: blocking another's path; taking objects others attempt to use.

In terms of of the evolution of playful teasing, what is the evidence for it among great apes? "Disentangling playful teasing from 'pure' play or aggression is challenging, as teasing is a highly ambiguous behaviour that straddles the border between play and aggression and can display behavioural characteristics of both" (Laumer et al 2024 p2).

Laumer et al (2024) investigated playful teasing by analysing video recordings of four captive ape groups - nine bonobos, four orang-utans, and four gorillas at San Diego Zoo, and seventeen chimpanzees at Leipzig Zoo. Over 75 hours of recordings were collected between 2016 and 2019.

In total, 142 teasing events were distinguished by three independent observers using a set of five behavioural criteria (eg: onesidedness - ie: action coming mostly from the teaser; surprise initiation (eg: target turned away); audience checking - ie: teaser looks at recipient's face). Five criteria of play were also

used for comparison. Eighteen types of teasing behaviours were classified, including offer and withdrawal of a body part or an object, play-hitting, pulling on a body part, and hindering the other's activity.

The researchers then sought the characteristics of playful teasing (eg: attention-getting; onesidedness). Intentionality of action appeared important: "Teasing was always directed towards a specific target. The teaser typically approached the target shortly before the first teasing behaviour. Teasers showed persistence when the targets ignored them (or only minimally reacted), typically by repeating their behaviour (in 84% of events), or elaborating by increasing intensity or switching behaviour (in 62% of events)" (Laumer et al 2024 p9). Juveniles were more likely than adults to playfully tease, and the majority of events occurred in relaxed contexts.

"From an evolutionary perspective, the presence of playful teasing in all four great apes and its similarities to playful teasing and clowning/joking behaviour in human infants suggests that playful teasing and its cognitive prerequisites may have been present in our last common ancestor, at least 13 million years ago" (Laumer et al 2024 p10).

The sample was small, both in number of (captive) individuals, and in observation time. The behaviour was categorised based on the interpretations of human observers, though independently and using agreed criteria. In pre-linguistic humans and apes it is difficult to know intention, whereas human adults can explain their reasons for playful teasing.

Reference

Laumer, I.B et al (2024) Spontaneous playful teasing in four great ape species Proceedings of the Royal Society B 291, 20232345

7. BEES SUFFERING

7.1. PESTICIDES

Pesticides and agro-chemicals (eg: neonicotinoids) are impacting pollinators, particularly wild bee reproduction and so their populations (eg: 40-90% reduction in offspring produced in neonicotinoid-exposed areas; Boff et al 2022).

Trap-nesting and underground nesting solitary bees are exposed to agro-chemicals with both direct and indirect effects. For example, neonicotinoids impact ovary development and reduce egg-laying ability, and males' spermatic cells are less viable (direct effects) (Boff et al 2022).

An indirect effect may be on pre-copulatory display. Boff et al (2022) showed this with the solitary horned mason bee (Osmia cornuta). Females evaluate the quality of competing males from thoracic vibrations and odours before choosing a single male to mate with. This is "scramble competition". Males exposed to a commonly used fungicide produced reduced vibrations and had an altered odour compared to controls, and were less successful at mating.

The basic design of the experiment was to give a virgin female (unexposed to the fungicide) a choice of males (exposed, half controls), and to measure the order of choice of males, the number of successful copulations per male, and the time spent copulating. A total 28 females were used with 68 males. Control males performed sixteen successful copulations to the 5-6 of exposed males, for example.

7.2. FEELING PAIN

"Nociception is the detection and processing of noxious stimuli1 and can be identified from recording neural activity or behaviour associated with the activation of nociceptive circuits. Insects have both nociceptors and nociceptive neurons that detect mechanical, thermal, and chemical noxious stimuli, and they respond behaviourally by moving away from and avoiding noxious stimuli" (Gibbons et al 2024 p1). "Self-

protective behaviour" includes tending to or rubbing a noxiously-stimulated body part, and self-grooming, commonly seen in many species.

Gibbons et al (2024) reported a study with the buff-tailed bumblebee (Bombus terrestris) (n = 82 participants). One antenna was briefly touched by a 65 °C heated probe or an unheated probe, and the subsequent behaviour of the bee was observed for 25 minutes. Bees self-groomed the touched antenna significantly more than the untouched one, irrelevant of the heated or unheated probe. But in the two minutes after touching, "bees groomed the touched antenna more than the untouched antenna when the touch was noxious" (Gibbons et al 2024 p3).

This was evidence of self-grooming behaviour in response to a noxious stimulus by an insect. There is limited evidence that insects generally do this behaviour (Gibbons et al 2024).

Was this behaviour evidence of bees feeling pain? Maybe. Self-grooming is known to reduce pain in humans, for example, and responding in this way requires brain processing (the antenna links directly into the bee's brain). On the other hand, there are animals that show reflexive behaviour (ie: via the spinal cord) to noxious stimuli (Gibbons et al 2024).

Gibbons et al (2024) concluded: "Our study shares with others (including those on vertebrates) the challenge that it is currently impossible to be certain about whether a behaviour includes the affective component of pain. Therefore, to assess whether an animal can feel pain, it is valuable to collect evidence from multiple different lines of neural, behavioural, and psychological investigations to shift probabilities for or against. Self-protective behaviour is included as one of eight criteria for the evidence of pain in other animals (Birch et al 2021; table 7.1). Before our study, Adult Hymenoptera already fulfilled four of these eight indicators of pain, namely they have nociceptors and sensory integrative brain regions, display motivational trade-offs, and learn from aversive experiences. Our study thus provides evidence for a 5th criterion, self-protective behaviour, so Hymenoptera might now be considered in this framework to show 'strong evidence for pain'" (p4).

The animal possesses:

- nociceptors.
- "integrative brain regions capable of integrating information from different sensory sources".
- neural pathways between nociceptors and integrative brain regions.
- biochemistry that affects response to noxious stimuli.

The animal shows:

- "motivational trade-offs, in which the disvalue of a noxious or threatening stimulus is weighed (traded-off) against the value of an opportunity for reward, leading to flexible decision-making".
- "flexible self-protective behaviour" (eg: wound-tending, rubbing or grooming bodily area impacted by noxious stimuli.
- "associative learning in which noxious stimuli become associated with neutral stimuli, and/or in which novel ways of avoiding noxious stimuli are learned through reinforcement".
- that "it values a putative analgesic or anaesthetic when injured" (eg: self-administer analgesic; prioritise analgesics over food).

(Source: Birch et al 2021 p17)

Table 7.1 - Eight criteria for evidence of pain in a non-human animal.

7.3. REFERENCES

Birch, J et al (2021) Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans London: LSE Consulting, London School of Economics and Political Science

Boff, S et al (2022) Low toxicity crop fungicide (fenbuconazole) impacts reproductive male quality signals leading to a reduction of mating success in a wild solitary bee Journal of Applied Ecology 59, 1596-1607

Gibbons, M et al (2024) Noxious stimulation induces self-protective behaviour in bumblebees iScience 27, 110440

8. THE THINGS MALES DO TO MATE

8.1. MISDIRECTED AMPLEXUS

Successful sexual reproduction requires recognition of conspecifics of the opposite sex, though sometimes hybridisation is possible. Heterospecific (misdirected) mating attempts have been observed in anuran amphibians (frogs and toads), mainly because amplexus (clasping a mate) (figure 8.1) can last for days, and "are relatively conspicuous as compared to secretive or short matings that are difficult to observe in many other taxa" (Brischoux and Lorrain-Soligon 2024 p529).

(Source: Bernie; https://commons.wikimedia.org/wiki/User:Bernie_Kohl; public domain)

Figure 8.1 - Amplexus by common toad.

As well as misdirected amplexus where a male grasps another male of the same species, and similarly

heterospecifics of both sexes, it has been observed with clasping of very different animals (eg: fish; turtle), dead individuals, and inanimate objects (Brischoux and Lorrain-Soligon 2024).

A number of explanations of misdirected amplexus have been proposed (or a combination of), including most importantly (Brischoux and Lorrain-Soligon 2024):

a) The breeding strategy - ie: "explosive" or "scramble competition". A very short breeding season (possibly the only one in a lifetime) where very competitive males are driven to find a small number of females as quickly and/or as often as possible).

b) Lack of discrimination - ie: an inability to recognise males or females of the won species or individuals of another species.

"In such conditions, it would be advantageous for males to arbitrarily be attracted to – and thus clasp – any female-looking object in order to increase mating probabilities... This is supported by the geographical distribution of species in which misdirected amplexus were more frequently recorded (Neartic and Palaeartic...). In these areas, suitable reproductive conditions are restricted in time, favouring explosive breeding and thereby promoting higher occurrence of indiscriminate amplexing behaviour" (Brischoux and Lorrain-Soligon 2024 p530).

Brischoux and Lorrain-Soligon (2024) investigated misdirected amplexus in the evolutionary history of anurans using a dataset from Serrano et al (2022), and updated. Statistical analyses were applied, and it was concluded that "the probability that misdirected amplexus occurred at the ancestral node of the current anuran phylogeny was very high" (Brischoux and Lorrain-Soligon 2024 p531). The persistence of the behaviour, though infrequent (based on human observations), and the cost of mating attempts with unfit mates is outweighed by the benefits of the "clasp anything quick" breeding strategy. "Overall, fierce competition in small water bodies during short breeding seasons is likely to promote relatively weak mate discrimination but, in turn, promiscuity induced by explosive breeding may decrease the costs of infrequent misdirected amplexus – and thus reproductive failure – at the population level" (Brischoux and Lorrain-Soligon 2024 p533).

Brischoux and Lorrain-Soligon (2024) admitted that

their data were sparse - 159 anuran species observed in misdirected amplexus out of 6700 total species (2.4% of total).

References

Brischoux, F & Lorrain-Soligon, L (2024) Anuran swingers: Misdirected mating attempts occurred early during anuran diversification Biological Journal of the Linnean Society 141, 529-536

Serrano, F.C et al (2022) Finding love in a hopeless place: A global database of misdirected amplexus in anurans Ecology 103, 8, e3737

8.2. SLEEP REDUCTION DURING THE BREEDING SEASON

Despite the importance of sleep, there are cases where animals can function with very little - for example, African elephants sleep for two hours per day and can go without sleep for nearly two days, or northern elephant seals who sleep two hours per day while diving (Zaid et al 2024) (table 8.1).

SPECIES	AVERAGE SLEEP (hours)	REDUCED SLEEP (hours)
Great frigatebird	12.8 (on land)	0.7 (flight while foraging at sea)
Northern elephant seal	10.8 (on land)	1.7. (foraging at sea)
Northern fur seal	6.4 (on land)	3.8 (at sea)

(Source: Lyamin and Siegel 2024 figure 1)

Table 8.1 - Examples of animals that show periods of reduced sleep.

Where there is a limited breeding season time-wise or a single reproductive period in the lifetime (semelparity), forgoing sleep is an important strategy to increase reproductive success (eg: male pectoral sandpipers who slept least during the three-week breeding season sired most offspring) (Zaid et al 2024).

The semelparity breeding strategy of the dusky antechinus (Antechinus swainsonii) and the agile antechinus (Antechinus agilis) sees the synchronous death of all males at the end of the only breeding season

(known as "mating syndrome") [9], though females may survive to a second season (Zaid et al 2024).

In these marsupials ("pouched mice"), during the breeding season, "males compete for access to as many females as possible to maximise reproductive success. Under these circumstances, the need for sleep might limit the time available to access receptive females, such that selection may favour males able to reduce sleep while maintaining the performance needed to forage, avoid predators, and secure mates" (Zaid et al 2024 pp606-607).

Zaid et al (2024) confirmed this view with data from fifteen dusky antechinus (including ten males) and 38 agile antechinus (of which twenty were males). Accelerometry (from back-mounted device), electrophysiological (laboratory brainwave recordings), and testosterone (in blood samples) data were collected. Only males increased their activity during the breeding season (and reduced their sleep time) (35% of the time active before the breeding season to 50% during it). "In a trade-off between the neurophysiological requirements for sleep and evolutionary necessity for reproduction, strong sexual selection might drive males to sacrifice sleep to increase access to fertile females and ultimately maximise their fitness" (Zaid et al 2024 p606).

The researchers could not establish if sleep loss was overcome by sleeping more deeply during the breeding season. "Sleep rebound" after the breeding period was not found (Lyamin and Siegel 2024).

Zaid et al (2024) argued against the synchronous death of males after the breeding season as due to excessive sleep loss, or elevated corticosteroids, "[I]nstead, there appears to be an unknown trigger from the natural environment as the cause of this synchronous 'programmed' death" (p612).

8.2.1. Semelparity

A number of theories for semelparity relevant here include:

i) Food availability not consistent across the year. The breeding season is when food peaks, but there are shortages the rest of the time which would make it very difficult for males to survive to the next year.

Or timed mating ensures offspring and weaned when food is abundant.

[9] Occasionally males survive, but they become sterile (Zaid et al 2024).

Related to this is that males are sacrificing themselves to allow their offspring to have the limited food ("altruistic paternal suicide").

ii) Sexual selection where females prefer young males.

iii) Extreme sperm competition - Longer copulation duration reduces the possibility of rival sperm, but it is physically demanding over two or three weeks (eg: three hours for agile antechinus; Kraaijeveld et al 2003).

References

Kraaijeveld, K et al (2003) Does female mortality drive male semelparity in dasyurid marsupials? Proceedings of the RoyalSociety of London Series B: Biological Sciences 270, Supp 2, S251-S253

Lyamin, O.I & Siegel, J.M (2024) Sleep: Giving it up to get it on Current Biology 34, R213-R216

Zaid, E et al (2024) Semelparous marsupials reduce sleep for sex Current Biology 34, 606-614

8.3. LIMB AUTOTOMY AND MATING STRATEGY

Limb autotomy is "the voluntary shedding of a body part at a pre-defined breakage plane when a stimulus is applied" (Powell et al 2023 p614), and it is a strategy used by some animals to escape predator attacks. For example, lizards lose their tail, crabs their claws, and long-legged harvestmen their legs. "In comparison to lizards and crabs, harvestmen are unique in that they are unable to regrow the lost limb... This means that resources and energy are not expended in regeneration, but also that other potential costs of autotomy are retained across the lifetime. The costs of leg loss in harvestmen include reduced locomotor performance..., reduced foraging ability..., and a disadvantage in male-male contests for territory possession" (Powell et al 2023 p614).

Powell et al (2023) investigated leg autotomy as a juvenile in the New Zealand long-legged harvestman Forsteropsalis pureora, and the impact on male-male contests for mates. This species has three types of males (morphs), differing in body size, and in weaponry (size and shape). "The morphs include a small-bodied male with tiny chelicerae ["jaws"] (gamma) (figure 8.2), a large-

bodied male with long-slender chelicerae (beta), and a large-bodied male with short but broad chelicerae (alpha), all of them co-existing within single populations. Alpha and beta males can have a body mass up to seven times higher than that of gamma males, demonstrating the drastic intra-specific variation found in this species. Gamma males adopt a scrambling strategy, searching through their environment to find mates and avoiding contests with other males, while alpha and beta males use their exaggerated chelicerae as weapons in contests to access females" (Powell et al 2023 p614).

Which leg is lost is also relevant. The first pair of legs ("legs I") are primarily for movement, but also have sensory functions, while the "legs II" pair are entirely sensory (known as "antenniform legs"), and "legs III" and "legs IV" locomotor appendages only. "Whereas the loss of a sensory leg may hamper food detection, the loss of locomotory legs may hamper food search" (Powell et al 2023 p615).

The researchers predicted that juveniles who lost a leg (or legs) would be more likely to develop into gamma males. Eighty-six males were collected from four sites in New Zealand in early 2018, of which 63 were classified as alphas or betas, and twenty-three as gammas. Examining the dead individuals under a microscope it is possible see if the limb loss occurred before or during adulthood. Overall, 83% of the gammas had juvenile autotomies compared to 10% of the other group. Loss of a sensory leg was more important than of locomotor appendage in becoming a gamma adult male.

In a species like this where there are different morphs, there is a trade-off during development. Increased foraging leads to a larger body size, but it also increased predator exposure. "The loss of legs owing to increased risk of predation may ultimately make developing into a major (alpha or beta) either unattainable due to lower access to nutritional resources or a poor strategy because males are at an immediate disadvantage in contests without fully intact legs" (Powell et al 2023 p616).

This study provided correlational evidence only - ie: between type of male and when in development the leg was lost.

(Source: Sceliphron/Erin Powell; creative commons attribution-share alike 4.0)

Figure 8.2 - Gamma male harvestman Forsteropsalis pureora.

Reference

Powell, E.C et al (2023) Juvenile leg autotomy predicts adult male morph in a New Zealand harvestman with weapon polymorphism Behavioural Ecology 34, 4, 613-620

8.4. COSTS OF KEEPING A HAREM

Mate defence polygyny is a breeding strategy where a dominant male will defend a harem of females from other males. The dominant male has exclusive mating rights with the harem, and the females therein benefit from genes from the "best" male in the population.

The density of a population impacts the level of male competition in three ways (Lloyd et al 2023):

i) Number of male competitors - More males means more challengers to the dominant individuals, who have to expand more energy and risk injury in male-male interactions.

ii) The relative number of females to males - Few

females increases the intensity of male competition.

iii) Male age structure - This is the number of males in each age class. "Generally, the competitive ability of males increases with age because of selection for high-quality individuals... and/or individual improvement due to experience... Therefore, competition intensity is reduced when older, experienced males are removed from the population (eg: through trophy hunting), causing younger, inexperienced males to allocate more resources to participate in current breeding events" (Lloyd et al 2023 p184).

Lloyd et al (2023) explored these ideas using thirty-four years of data on Southern elephant seals (Mirounga leonina) at Marion Island, in the sub-Antarctic Indian Ocean (administered by South Africa). Since 1983 all pups born have been tagged. Complete data were available for 291 males.

"Male elephant seals compete for dominance of female harems over an annual 3-month breeding season during which they do not supplement stored body reserves... Thus, males display an extreme form of capital breeding by allocating only stored body resources into an intense and relatively long breeding event... Social dominance is often determined by body size (for winning fights) and resource-holding potential (for fasting endurance...). Dominant males defend their mating rights from subordinate males and service oestrus females regularly... Competition for mates is generally intense as only a small fraction of recruited males become dominant... Subordinate males may employ 'sneaking' tactics to mate with females, but this is relatively infrequent compared to dominant male paternity rates... Thus, social status can be a reliable proxy of reproductive success for this species" (Lloyd et al 2023 p184).

The number of females in a harem relative to the average was found to be key in terms of reproductive costs for a male. These costs include pre-copulatory competition (male-male interactions), and post-copulatory competition (eg: more sperm allocated to each ejaculate). In other words, males with larger harems spent more time and effort (measured as weight loss) defending and servicing the females, and less on body maintenance (leading to earlier mortality). This supported the "disposable soma theory of senescence" (Kirkwood and Rose 1991), which proposes that "males increase resource allocation to optimise reproduction under harsh

environmental conditions (here in the form of competition intensity) at a greater cost to self-maintenance" (Lloyd et al 2023 p189). Dominating a large harem at a younger age also increased earlier mortality.

But dominant males had higher survival probabilities than subordinates, controlling for variables like age. Survival and death were based on a male returning the next breeding season.

Applying population density to the equation, it was found that males born in years with few pups were more likely to become dominant, and to start a harem at an earlier age than in years with many pups. This supported the "silver spoon hypothesis" (eg: Grafen 1988). Thus, population density during early life was important.

References

Grafen, A (1988) On the uses of data on lifetime reproductive success. In Clutton-Brock, T.H (ed) Reproductive Success Chicago: University of Chicago Press

Kirkwood, T.B & Rose, M.R (1991) Evolution of senescence: Late survival sacrificed for reproduction Philosophical Transactions of the Royal Society B 332, 15-24

Lloyd, K.J et al (2023) Density-dependent reproductive costs and natal conditions predict male life history in a highly polygynous mammal Animal Behaviour 200, 183-197

8.5. PRE-COPULATORY MATE GUARDING

Schausberger et al (2023) stated: "Intense mate competition favours the evolution of extraordinary mating strategies such as the ability of males to identify premature females that are close to becoming mature and associate with them until they are sexually receptive (dubbed pre-copulatory mate guarding). Owing to possible take-overs by rival males, pre-copulatory guarding is a high-risk, time- and energy-intensive strategy" (p1).

Pre-copulatory mate guarding evolves in species with a short time window to fertilise females, monandry (one mating partner in life or per breeding season), and/or where the first male's sperm has precedence (Schausberger et al 2023). It has been seen in crustaceans, butterflies, and mites, for example.

Because of the costs of pre-copulatory mate guarding, strategies should evolve to shorten the duration of guarding and increase the certainty of the guard to fertilise the female. For example, some male

butterflies practice "pupal mating" and inseminate the female still covered by her pupal case (Schausberger et al 2023).

Another strategy, reported by Schausberger et al (2023), and used by two-spotted spider mites (Tetranychus urticae) (figure 8.3) is "undressing the female" (ie: actively accelerating ecdysis). Ecdysis is the process of casting off the harden cuticle to become an adult. In an experiment, thirty guarded females were found to eclose (emerge from the pupae) significantly faster than 34 unguarded females (mean approximately 4 vs 8 minutes). Guard males were observed to drum on the female dorsum with their forelegs to stimulate the cracking of the exuvia (outer skin) and to allow access to the genital opening. "Eagerness in undressing may indirect benefit females if this behaviour is indicative of male quality and females adjust their accessibility accordingly" (Schausberger et al 2023 p2).

(Source: Tomas Pocius; public domain)

Figure 8.3 - Two-spotted spider mite.

The experiment did not include a rival male to the guard to see that impact on the "undressing",

particularly the success of the guard in being the first mating. Schausberger et al (2023) were interested, for future research, "whether sneaker and fighter males, which both guard premature females, differ in undressing behaviour" (p3).

Reference

Schausberger, P et al (2023) Spider mite males undress females to secure the first mating iScience 26, 107112