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More 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. SPERM COMPETITION IN BUTTERFLIES

1.1. SPERM COMPETITION

Sperm competition (Parker 1970) is "the competition, between the sperm of more than two males who have mated with the female, for fertilisation of the eggs in the female internal reproductive organs" (Watanabe 2016 p1).

Female insects can store sperm (in the spermatheca) until required to fertilise the eggs, and so "insect sperm must retain its fertilisation capacity throughout the lifespan of the female, and the females are able to fertilise eggs using the stored sperm for oviposition at any time" (Watanabe 2016 p1).

Female butterflies are mostly polyandrous and so will mate with multiple males. The upshot is the presence of sperm from different males together in the female sperm storage organs, resulting in sperm competition. After copulation, the female receives the spermatophore in the bursa copulatrix, and so "it is easy for researchers to count the number of spermatophores by dissection of the female abdomen. Each spermatophore is the result from a single successful copulation, indicating that the number of spermatophores equals the number of matings in the female" (Watanabe 2016 p2). The spermatophore is a protein-rich capsule that encloses the sperm, and is digested by the female for energy.

Traditional behaviours by males as part of sperm competition include guarding the female after copulation to stop rival males from mating, the placing of a "mating plug" in the female genitalia, the transfer of anti-aphrodisiac substances to the female, or the removal of rival sperm already present inside the female (table 1.1) [1] [2]. Mate guarding is not feasible in butterflies because the female moves around dispersing the eggs onto different plants (as a risk-spreading strategy). The size

[1] Around the animal kingdom, there are penile brushes and scrapers to remove rival sperm, seminal secretions that disable its movement (eg: fruit flies), the use of flooding with large numbers of sperm (eg: crickets), or producing more competitive sperm than rivals (eg: nematode) (Watanabe 2016).

[2] "However, the morphology of female reproductive organs in butterflies shows that males are not able to directly manipulate the sperm of previous males in the spermatheca, because the spermatheca is completely separate from the bursa copulatrix where the spermatophore is formed during copulation" (Watanabe 2016 p122).

of the spermatophore, however, is important. There is a short period after mating when the spermatophore is digested and the female does not copulate during this period, so "one of the male's strategies to inhibit re-mating of his mate is an increase in spermatophore size, in which the female could receive much more nutrient" (Watanabe 2016 p3). The production of the spermatophore is costly for the male (eg: requiring 2-3 days feeding on nectar) (Watanabe 2016).

- Mating (or nuptial) plugs (also known as sphraga) are additional gland secretions that harden in the female's copulatory opening, and stop later males from mating. "Because female butterflies have two genital openings, males can block the copulatory opening without hindering oviposition. Therefore, no other male can gain access, but females can oviposit" (Watanabe 2016 pp113-114). Some plugs can be large enough to be visible to other males. But the plug may dissolve or fall out, and the female can remate.

- Anti-aphrodisiacs - For example, in the queen butterfly (Danaus gilippus), "males release a pheromone-bearing dust from their hair-pencils containing a flight inhibitor and a glue that sticks the inhibitor onto the female's antennae, reducing their attractiveness. Consequently, the pheromones reduce the likelihood that the female will mate again, and also reduce costly harassment by additional males, which is beneficial to the females" (Watanabe 2016 p114).

- Prolonged copulation is a "male in-copula guarding strategy" (Watanabe 2016 p125). The male determines when to stop copulation, and spermatophore transfer occurs immediately, so "his body acts as a nuptial plug and impedes additional copulations of the female" (Watanabe 2016 p125). It has been observed that when copulating pairs are harassed by single males, the copulation duration is increased (Watanabe 2016). A female response is to avoid time-consuming matings by refusal postures, or, in the case of pale clouded yellow (Colias erate), by mimicking males (Watanabe 2016).

Table 1.1 - Sperm competition strategies

In terms of sperm competition within the female body, two different types of sperm have been found in butterflies - eupyrene and apyrene sperm. The former is used for fertilisation while the latter has no nuclear body (Watanabe 2016). Apyrene sperm is believed to play a role in sperm competition. For example, the number of apyrene sperm has been shown to increase the refractory period of female re-mating (Cook and Wedell 1999).

A number of theories have been proposed for the function of apyrene sperm, which Swallow and Wilkinson (2002) grouped into:

i) Provisioning - The apyrene spermatozoa provide nutrients within the female reproductive organs for the eupyrene spermatozoa, for the female, or the ovum.

ii) Facilitation - The apyrene spermatozoa facilitate the movement of the eupyrene sperm from the testes or within the female reproductive organs.

iii) Competition - They play a role in sperm competition with other male's sperm in the female reproductive organs, either by eliminating or disabling previous sperm, blocking later sperm entry, or delaying remating.

iv) Other, or no function.

Most butterfly species are unable to remove rival sperm as the penis cannot reach where the eupyrene sperm is stored. But "the transfer of a large ejaculate by the male can counter the effects of sperm competition directly by diluting or displacing rival sperm, thereby increasing the proportion of the female's eggs fertilised by the male, or indirectly by extending the duration of the female's post-mating refractory period, or by increasing the rate of oviposition following mating. However, because females absorb spermatophore nutrients, the spermatophore size begins gradually to decrease about 2 days after copulation" (Watanabe 2016 p115).

"Last-man priority" (or sperm precedence) has been observed in most butterfly species. This is the advantage of the sperm of the second mating male being closer to the fertilisation duct (Watanabe 2016). For example, in the cabbage white (Pieris rapae), males transfer more eupyrene sperm, but a smaller spermstophore, at second mating (Cook and Wedell 1996).

Calculations have been made of the proportion of eggs fertilised by the second male in a double-mating situation ("P_2") (eg: 0.86 for mocker swallowtail (Papilio dardanus); 1.00 for the alfalfa butterfly (Colias eurytheme); Simmons and Savia-Jothy 1998).

Males seem to be able to control the number of sperm transferred (known as "strategic copulation"). "The virgin males seem to have an ability to keep some sperm for further matings, whereas the mated males transfer most of the sperm in their sperm storage organs at the their second mating, irrespective of the number of sperm stored" (Watanabe 2016 p128).

Watanabe and Kobayashi (2006) compared the spermatophore of two species of swallowtail butterfly - Asian (Papilio xuthus) (which is polyandrous), and Old World (Papilio machaon) (which is monandrous). The weight of the former was 2.4% of the male's body compared to 2.1% in the latter species. The sperm of the male of the polyandrous species contained 41 eupyrene sperm bundles and 247 000 apyrene spermatozoa compared to 120 and 202 000 respectively (Watanabe 2016).

Length of adult lifespan is relevant as this influences opportunities for more matings. Female quality is further variable. Reinhold et al (2002) simulated sperm allocation in successive matings in four scenarios that varied female quality and that males could detect that variety. "The simulations predicted that males should invest more sperm in the first copulation than subsequent copulations and more sperm in high-quality females than in low-quality females. However, with increasing variance in female quality, males could conserve more sperm for later copulations" (Watanabe 2016 p130).

1.2. CRYPTIC FEMALE CHOICE

"For success, a female butterfly has to develop eggs, to mate, to be inseminated and then to place those eggs in sites where there is the greatest likelihood of larval survival. Because early-instar larvae have little choice as to what they eat and depend on the judgement of the female to place eggs, females are highly selective in their choice of larval host plants. In searching for an egg-laying site, females have to respond to several specific demands that will affect the survival of their offspring" (Watanabe 2016 p135). Choosing the best sperm/mate is part of this process, and it is known as "cryptic female choice".

Criteria used by females include male body size, ejaculate size, age, and mating history (Watanabe 2016). Evidence that a decision is being made is the observation that female green-veined whites (Pieris napi) who mated first with a small male remated sooner than when first mating was with a large-sized male (Watanabe 2016).

In terms of mating history, it has been suggested that "females are able to detect the cues of males from previous mates and use this information to avoid mating with sperm-exhausted males" (Watanabe 2016 p146).

A post-copulation cryptic female choice is sperm ejection. "There is insufficient evidence regarding how females compare the ejaculate size of the first and the second males, although females seem to be able to measure the size of ejaculate using stretch receptors in the wall of the bursa copulatrix" (Watanabe 2016 p151).

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2. ANIMAL RESEARCH ETHICS

2.1. INTRODUCTION

Research at Harvard University by Margaret Livingstone (eg: Arcaro et al 2020) on how the primate brain processes faces has drawn criticism. Newborn monkeys were removed from their mothers, and some had their eyelids stitched shut, in both cases so that no faces were seen for the first year of life (Grimm 2022) (table 2.1).

A letter was written by primatologist Catherine Hobaiter and over 250 others to the US journal "Proceedings of the National Academy of Sciences" in October 2022 asking for Livingstone's article to be retracted. Others, however, have defended such methods and studies (Grimm 2022).

- Macaques hand-reared by humans who wore welders' masks to prevent the faces being seen (n = 4), or "binocular-visual-form deprivation via eye lid suturing" (p32676) (n = 2) for the first year.

- All macaques with healthy or deprived visual world had surgical implanting of micro-electrodes in areas of the brain to measure electrical activity when shown faces.

- After the experiment, participants euthanised to allow post-mortem study of the brain.

Table 2.1 - Key details of Arcaro et al (2020).

2.2. CLASSIC RESEARCH

Harlow and Zimmermann (1959) are best known for experimentally testing the attachment of infant macaques by offering different surrogate mother models. Livingstone (2022) explained: "Some surrogates were soft and others rigid and unyielding, with or without faces, heated or not, with or without an attached milk bottle. Infants provided with two different surrogates overwhelmingly preferred the cloth surrogate over the rigid surrogate, irrespective of which provided milk or heat or had a face. Infants displayed strong sustained attachment to and derived security from cloth surrogates for more than a year and a half (the duration of the experiment). Infants' attachment to and behaviour toward the cloth surrogates was indistinguishable from mother-reared infants' attachment to their monkey mothers" (p2).

This work showed the importance of physical attachment, and this helped in challenging the prevailing view with hospitalised children which was to keep them physically isolated. Livingstone (2022) reported: "Both my collaborator, David Hubel, and my husband recollect being hospitalised as young children and not allowed visitors; their mothers could only wave to them through a window in the door. Both found it traumatising" (p1).

Margaret Livingstone studied the other side of the attachment, the mothers, and found that tactile cues were key. She described the chance beginning of the research: "My first observation was of an 8-y-old primiparous female rhesus macaque, monkey Ve. She delivered a stillborn infant. She was holding the lifeless infant to her chest when I first observed her in the morning. Appropriate veterinary care required that the dead infant be removed and examined, and to accomplish this, she was lightly anaesthetised. When she recovered a few minutes later, she exhibited significant signs of distress: She vocalised loudly and constantly and seemed to be searching agitatedly around her enclosure. Other monkeys housed in the same room also began to vocalise and became agitated. To try to reduce the level of stress in the room I placed a stuffed animal in her enclosure. It was a 15-cm-tall, soft, furry toy, a faceless stuffed mouse, chosen because of its availability and its lack of potential choking hazards, such as sewn-on eyes. Monkey Ve immediately picked up the stuffed toy and held it to her chest. She stopped screeching and became calm while holding it, and the whole room quieted down. She held the toy to her chest continuously for more than a week, without any signs of distress. During this time, she behaved in a manner indistinguishable from other mothers in our colony with live infants, in that she continuously held the toy to her chest, and she exhibited aggressive behaviour toward co-housed monkeys and toward even familiar humans when they approached her. This enhanced level of defensive behaviour is characteristic of females with infants" (Livingstone 2022 p2). Subsequent experiments were performed along the lines of Harlow and Zimmermann (1959) (Livingstone 2022).

2.3. NEW APPROACH METHODOLOGIES

Home Office figures showed that over three million experiments on animals took place in Britain in 2021. There was an increase in the use of monkeys, and dogs, in particular (Latest News 2022).

Hutchinson et al (2022) referred to the replacement of animal experiments as "modernising medical research". This involved the use of "New Approach Methodologies" (NAMs). These are those that can replace the use of animals in biomedical research (eg: "organ-on-a-chip"; organoids) [3]. There is evidence of increasing use of NAMs. Courtot (2022) surveyed scientific citations for six organs of study (lung, brain, heart, gut, kidney, and pancreas) for 2019 to 2022.

Hutchinson et al (2022) proposed four strands to their argument for modernising medical research:

i) The scientific case - Animal models of human diseases are not reliable because the animals used "often do not naturally suffer from the illness that is being investigated. This results in efforts to artificially induce some symptoms of the disease, whether by physical means or genetic modification" (Hutchinson et al 2022 p2).

ii) The ethical case - "It has been argued that the practice of animal research involves an inherent contradiction. It relies on the belief that animals are similar enough to humans to make the results relevant, but that they are different enough to make it morally acceptable to harm them in the pursuit of human benefit. In fact, there is strong evidence to show the opposite: that animals are different in all the ways that make extrapolation of data to humans unreliable, but are so similar in their capacity to experience suffering that this makes a formidable ethical case to not do animal experiments at all, regardless of any proposed human benefit" (Hutchinson et al 2022 p3).

iii) The economic case - The creation of drugs is an expensive process from discovery to marketing, and better disease models "could help to reduce the current rates of drug failure, and could potentially have a positive impact in lowering the cost of these new medicines"

[3] One definition of NAMs is "new scientific approaches that focus on human biological processes to investigate disease and potential treatments, using human cells, tissues, organs and existing data" (Alliance for Human Relevant Science quoted in Hutchinson et al 2022).

(Hutchinson et al 2022 p5).

iv) Public support for modern medical research - Public opinion polls by "YouGov" in 2021, for instance, found majority support for alternatives to the use of animals in medical research, and the ending of their use in experiments (Hutchinson et al 2022).

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3. COLLECTING DATA IN DIFFERENT WAYS AND SITUATIONS - SOME EXAMPLES

3.1. KLEPTOPARASITISM OF LYNX BY JACKALS

The concept of "invasive species" is often taken to mean those introduced either deliberately or accidentally by humans. But it also includes "naturally-expanding native species beyond their historic ranges" (Krofel et al 2022 p1), like golden jackals (Canis aureus) in Europe. This "expansion is raising many concerns among researchers and managers about the possible negative impacts towards local wildlife, including the reduction of ungulate populations and threatened birds, transmission of diseases and parasites, as well as hybridisation with other canids" (Krofel et al 2022 p1).

One potential consequence is food stealing (kleptoparasitism) by jackals of prey killed by apex predators like the Eurasian lynx (Lynx lynx). Krofel et al (2022) analysed data from the Northern Dinaric Mountains in Slovenia. Three historical periods were distinguished:

a) 1950-1970 - low lynx and jackal numbers (no overlap in territories).

b) 2000-2011 - increasing lynx populations and expanding jackal populations generally (small overlap).

c) 2012-2018 - expansion of jackals across Europe (larger overlap - estimated at 13%).

The data came from video surveillance, GPS telemetry, and previous studies. The former data included camera traps on sixty-five lynx kill sites in 2006-21. Jackals were observed at 3% of all kills surveilled (most in the last two years). These are "the first cases of scavenging on prey remains of lynx. Although it could not be established whether the lynx abandoned these kills before the arrival of jackals or if abandonment could be connected with jackal presence..." (Krofel et al 2022 p4).

Historically, the two species have not interacted, "in the last two decades and especially since 2011, trends in distribution patterns showed that the overlap between them is increasing rapidly, mainly due to extensive expansion of jackal populations, but also due to recovery of lynx in some parts of Europe" (Krofel et al 2022 p4).

It is not clear if the lynx will be able to successfully defend its kills from jackals. Other scavengers have overcome the lynx (eg: brown bears) or risked death (eg: red foxes) to take the killed prey. Also jackals can form large groups (eg: up to twenty individuals) (Krofel et al 2022).

Grey wolves may be a solution to control jackals, and they tend not to take lynx kills (Krofel et al 2022).

3.2. TREE CLIMBING TOADS

Temperate region amphibians tend to be terrestrial, while arboreal amphibians are more common in tropical regions (Petrovan et al 2022).

But a report of a toad found in a dormouse nest box in England in 2016 has raised interest in arboreal amphibians in the UK. Petrovan et al (2022) investigated this topic by analysing data from two citizen science surveys:

i) National Dormouse Monitoring Programme (NDMP) - 640 sites monitored between 1988 and 2014, checked twice a year. Amphibians were not consistently reported, so Petrovan et al (2022) sent on an online data request to NDMP surveyors.

ii) Bat Tree Habitat Key (BTHK) project - Begun officially in 2010 (though data since 2002) on roost sites.

A small number of observations of amphibians were found, of which the common toad (Bufo bufo) was most frequent. "The collated data from arboreal mammal surveys in Britain demonstrates that some amphibian species regularly climb trees in Britain and do so across their active period in the year, although with an apparent increase during summer and autumn months" (Petrovan et al 2022 p11).

On the positive side, the toads are "potentially attracted to tree cavities and arboreal nests because they provide safe and damp micro-environments which can support an abundance of invertebrate prey..." (Petrovan et al 2022 p1). But, on the negative side, they are "morphologically a typical terrestrial anuran, with short legs keeping the body close to the ground, slow walking or hopping movements and heavy body weight, especially for adult females, but which has been described as a 'laborious climber' which can overcome many obstacles on its way, particularly during the spring migration to the breeding ponds" (Petrovan et al 2022 p11).

A researcher in northern Spain (Gosa 2003) collected over 200 observations of local toads climbing trees between 2000 and 2003.

3.3. WHALES TRAVEL

Humpback whales are known to spend the winter (November-May) in two regions - along the Baja California Peninsula, Mexico, and around the Hawaiian Islands. These two areas are separated by 4500-6000 km, and so it was assumed that the whale populations were separate. "In 2016, the US National Marine Fisheries Service (NMFS) went significantly further, to designate the Mexico and Hawaii assemblies as Distinct Population Segments (DPS). The whales within each region were given different conservation status under the Endangered Species Act: Mexico 'Threatened' and Hawaii 'Not at Risk' — inferring biologically separate entities" (Darling et al 2022 p2).

But Darling et al (2022) provided evidence to challenge this idea as two whales were observed moving between the two areas in the same winter season (table 3.1). The researchers used photo-identification of individual whales by "the unique and permanent skin pigment patterns on the underside of the flukes" (Darling et al 2022 p2). Data on over 26 000 individuals from 1977 to 2020 were available (from the "Happywhale" project [4]).

Other sightings have been made at both sites, but not with the certainty of the two males (Darling et al 2022). The researchers ended: "Evidence of mixing between the whales that compose the Mexico and Hawaii populations is indisputable; the question now is one of significance. Is the mixing a rare occurrence with negligible biological impact or management consequence, or is it a reflection of a biologically meaningful integration of humpback whales throughout the northeast Pacific — if not the entire ocean basin?" (Darling et al 2022 p6).

[4] See https://happywhale.com/.

- Male A (in 2006) - seen off island of Maui (Hawaii) (23rd February), then off Isla Clarion (Mexico) (17th April).

- Male B (in 2018) - south of Zihuatanejo Guerrero (Mexico) (16th February), then off West Maui (Hawaii) (6th April).

Table 3.1 - Two whales that travelled between the two wintering grounds.

3.4. FENNEC FOXES IN ZOOS

"Ambassador animal" is a term used to describe an animal that directly interacts with visitors at zoological institutions (Kozlowski et al 2023).

How do such interactions impact on the animals? The "relatively few studies of ambassador animal welfare have reported mixed results" (Kozlowski et al 2023 p420). For example, bottlenose dolphins were found to have greater behavioural diversity (positive impact), while other species show signs of stress (eg: armadillos being handled) (negative impact), and some species appear unaffected (eg: camels) (Kozlowski et al 2023).

"Because no single method can reliably quantify animal welfare, researchers rely on a variety of measures to assess stress... While a number of physiological techniques exist, glucocorticoid production, usually quantified from faeces, is one of the most common measures used in zoo-based welfare studies... Glucocorticoids are secreted by the adrenal cortex in response to excitatory and stressful stimuli, and modulate responses to maintain homeostasis... Chronic increases in glucocorticoid production may be evidence of compromised welfare" (Kozlowski et al 2023 p421).

Kozlowski et al (2023) studied glucocorticoid production [5] in fennec foxes (Vulpes zerda) (figure 3.1) serving as ambassador animals, and the interaction with circadian activity patterns, and personality traits of the individuals. Thirty-five foxes at three institutions in the USA were studied [6]. There were three groups of animals - ambassador (shown close-up to visitors who could touch them while being held by a staff member) (n = 11) (table 3.2), exhibit (housed for public viewing) (n = 7), and off-exhibit (housed in pairs for breeding [7]) (n = 19) [8].

[5] Technically, faecal glucocorticoid metabolite (FGM) concentrations.

[6] Bronx Zoo, Saint Louis Zoo, and "Exotic Endeavours" (Santa Rosa, California).

[7] Ambassadors were housed in same-sex pairs or groups, and exhibit animals in same-sex pairs.

[8] Two foxes changed groups during the two study periods.

(Source: LadyofHats; public domain)

Figure 3.1 - Sleeping fennec fox in a zoo.

- During the programme, "foxes were transported by hand to a room down the hall from their enclosure, or in a crate to a classroom located at the zoo, and presented to a group of visitors (>10 to 35+). Visitors were given the opportunity to touch the fox while it was held by a staff member. During ambassador programs, foxes were presented to the public for 10-20 minutes before being returned to a crate or the animal's home enclosure. Ambassador foxes at Bronx also participated in periodic play sessions, which consisted of being transported by hand to a room with their enclosure-mates and allowed to roam without visitors present" (Kozlowski et al 2023 pp422-423).

Table 3.2 - Details of the ambassador programme at the Bronx Zoo.

Faecal samples were collected during two periods (November 2014 - March 2015 (winter), and May - August 2015 (summer)), and activity levels of the animals were measured by pedometers in collars (divided into number of one-minute intervals active), and from video recordings (table 3.3). Each animal was scored by their caretakers on twenty-two characteristics (eg: "aggressive to foxes", "shy", "playful") to give two dimensions of personality - sociable and dominant (table 3.4). Eighty-four characteristics were collected from the literature, and the researchers and other experts "eliminated items that were not relevant or redundant, and clarified or eliminated terms that seemed too subjective" (Kozlowski et al 2023 p425). At least two caretakers per animal scored each characteristic from 1 ("Not at all like this animal") to 5 ("Very much like this animal").

- Run - "Locomotion at a face pace, with only 1-2 feet on the ground at one time".

- Rest - "Individual is not moving; lying down, standing or sitting are all considered rest".

- Walk - "Locomotion at a slow pace in which 3 feet are supporting the body at all times. Only 1 foot is lifted from the ground at time in a regular sequence, amy co-occur with shake".

(Source: Kozlowski et al 2023 table 3 p426)

Table 3.3 - Example of 11 activity categories and definitions.

SOCIABLE	DOMINANT
Exuberant - "Energetic, enthusiastic; interacts with foxes or people with ears relaxed, tail wagging, vocalisations, and rolling on side or back". Confident - "Behaves in an assured manner; not easily intimidated, moves in a relaxed way". Playful - "Initiates play and joins when play is solicited".	Aggressive to people - "Causes harm or threatens to cause harm to people by barking, growling, lunging, biting, attempting to bite, or chasing". Aggressive to foxes - "Causes harm or threatens to cause harm to other foxes by barking, growling, lunging, biting, attempting to bite, or chasing". Moody - "Moods change quickly and unpredictably (including changes in a positive direction).

(Source: tables 3 p426 and 5 p431 Kozlowski et al 2023)

Table 3.4 - Examples of personality characteristics (with definitions) linked to each dimension.

No relationship was found between glucocorticoids in faeces and handling as ambassadors, and there was no difference in concentrations between the three groups. "Ambassador foxes tend to be hand-reared and receive extensive training and handling prior to interacting with the public, which may reduce future fear responses" (Kozlowski et al 2023 p432). However, there were significant differences between the three institutions, which "could indicate greater physical activity or potentially stress, and might be attributed to differences in environmental conditions, husbandry, or diet..." (Kozlowski et al 2023 p432).

In terms of activity levels, the only difference found was that ambassadors were more active throughout the day than the off-exhibit foxes. The researchers admitted that "it is not possible to know if higher activity resulted from a greater frequency of behaviours considered positive, negative, or neutral" (Kozlowski et al 2023 p432). Activity levels did not vary between the groups at night, when fennec foxes are traditionally most active. There were seasonal, and gender differences in activity levels observed.

Ambassadors scored higher on sociability than the other two groups, as did hand-reared over parent-reared animals. More sociable individuals had lower glucocorticoid measures (ie: less stressed). It was not clear if more sociable individuals became ambassadors or whether being an ambassador increased sociability. The researchers leaned towards the benefits of the latter - ie: "that frequent interactions with caretakers may influence confidence, playfulness and other aspects of behaviour" (Kozlowski et al 2023 p434).

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4. AMPHIBIAN IMMUNITY

Assis et al (2023) began their introduction to a special issue of the journal "Philosophical Transactions of the Royal Society B" on amphibian immunity with this outline of the situation: "Amphibian population declines and extinctions have been reported worldwide. In addition to environmental changes like temperature shifts, changes in rainfall regimes, loss of habitats, fragmentation, pollution, infectious diseases significantly contribute to this scenario. In addition, there are a multitude of documented shifts in behaviour and physiology that occur in native populations dealing with climate change and infectious diseases, which have been associated with alterations in hormonal and immune modulation, possibly leading to systemic failure and death" (p1).

Stress can be observed in animals by increased plasma glucocorticoid levels, and this has been reported in amphibians in recent years (Assis et al 2023). Glucocorticoids (eg: corticosterone) are hormones released into the blood as part of the "fight or flight" response to a stressor. In the short term, the body is enhanced (including the immune response), but continuous long-term stress leads to immunosuppressive effects (Assis et al 2023).

Stressors can impact the immune function in a number of ways including "changes in the number and type of immune cells produced, the speed and strength of immune responses and the susceptibility of individuals to diseases" (Assis et al 2023 p4).

Heat and dehydration are two key stressors which produce immune suppression (Rollins-Smith and Le Sage 2023). On the other hand, bullfrogs showed faster wound healing (compared to controls) with experimentally increased corticosterone levels in the first 48 days, but slower after that (Madelaire et al 2023).

Miller et al (2023) experimentally reduced microbial richness and diversity in the gut of tadpoles of the African claw frog, and found that the adults were more susceptible to disease.

The interaction between an organism's immune system and its environment is studied in eco-immunology. This is "an inter-disciplinary field integrating concepts and methods from ecology, evolution and immunology. Eco-immunology seeks to understand how the immune system of an organism adapts to environmental conditions and stressors, such as temperature, food availability and exposure to pathogens. It also examines how immune responses influence the fitness and survival of individuals, populations and species" (Assis et al 2023 p4).

Real-world data on naive multi-host amphibian communities and novel pathogens are rare, but Longo et al (2023) reported "a unique epidemiological dataset obtained during an outbreak of chytridiomycosis, caused by the fungus Batrachochytrium dendrobatidis (Bd), at a species-rich cloud forest amphibian community at El Cope, central Panama" (p1) in 2004. Seventy-four species of amphibians existed there before the outbreak, more than 80% were infected, and thirty species disappeared.

The fungus suppresses the immune system and so make the infected individual vulnerable to other pathogens. Aquatic breeders (ie: those with aquatic larvae) were more likely to be infected and vulnerable (four times more likely than terrestrial breeders). This is the reproductive mode.

Tolerance and resistance are two important concepts in immunity. "Tolerance measures an animal's ability to limit detrimental effects from a given infection, whereas resistance is the ability to limit the intensity of that infection" (Grogan et al 2023 p1). Resistance protects the host at the cost of the pathogen, while tolerance does not harm the pathogen (Grogan et al 2023).

Tolerance mechanisms exist at the cellular, tissue/organ, and whole body (systemic) level. Bd (and Batrachochytrium salamandrivorans; Bsal) attack directly by invading epidermal tissues, and result in the the skin being compromised. They also cause indirect damage by release of toxic and immunosuppressive substances. Tolerance here involves combatting the two modes of attack (eg: tissue regeneration and repair; release of anti-bodies) (Grogan et al 2023).

Risk of infection is based on exposure to the pathogen, and variables here include type of habitat (eg: aquatic or terrestrial), time spent there, and temperature (Grogan et al 2023). Alpine newts, for example, have shown a change in behaviour to drier environments to avoid infection (Daversa et al 2018).

The idea of viral load is also relevant. This is the suggestion that an equilibrium between the animal and the pathogen is reached, such that the animal can continue their life. But it means that the animal could be a spreader of the pathogen. For example, tolerant infected tadpoles maintain the pathogen in a stream, and adults are exposed to infection when they come to the stream to breed. This is even worse with long-lived tadpoles (ie: 1-2 years to metamorphose). The stream in this case is an "environment zoospore pool" for the pathogen (Grogan et al 2023).

"Simple theory suggests that because tolerance increases the force of infection, tolerant hosts have a fitness advantage as infection prevalence increases, promoting selection for tolerance traits, and thereby increasing their frequency within a population over an evolutionary timeframe" (Grogan et al 2023 p7). This is the "tolerance fixation hypothesis" (Roy and Kirchner 2000).

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5. BIRDS

5.1. A and B EGGS

The erect-crested penguin (Eudyptes sclateri), which breeds on the Bounty and Antipodes Islands (south-east of New Zealand), is "by far the world's least studied penguin species" (Davis et al 2022 p2). They lay two eggs separately; the first egg ("A-egg") in early October and a larger second egg ("B-egg") about one week later. "Some observations suggest that the A-egg may be broken, rolled away or even deliberately ejected by the female, with typically only the B-egg being incubated" (Davis et al 2022 p2).

The difference in egg size may range between 25 and 70%. "Such extreme egg-size dimorphism facilitates asynchronous incubation and hatching, and is associated with obligate brood reduction" (Davis et al 2022 p3).

What is the function of the A-egg? One answer is as a form of insurance against loss of the B-egg. But A-eggs are often lost before the B-egg is laid, and in other species using an insurance strategy, "the extra smaller egg is usually the last-laid egg" (Davis et al 2022 p3).

Other explanations include "suggestions that it reduces costs due to fighting during the courtship period, functions as a visual signal of occupied nest sites or facilitates laying synchrony within a colony - although these explanations have not been tested" (Davis et al 2022 p3).

Davis et al (2022) addressed the function of the A-egg with observational data from Antipodes Island in 1998, which included 270 banded individuals in a single study colony. An experimental colony of 42 nests was also created where stones were placed around the nest to stop the A-egg rolling away.

A-eggs were lost before the B-egg was laid (42%), or on the day of laying the B-egg (38%). The remainder of A-eggs did not survive seven days after the B-egg was laid.

The researchers offered this possible explanation for the A- and B-eggs, pointing out "these are offshore foraging penguins that probably cannot bring enough food back to the nest to rear two chicks. Erect-crested penguins are derived from ancestors that laid two-egg clutches and, theoretically at least, it would have been possible to reduce clutch size by simply stopping laying another egg after the first one, had selection favoured the first-laid A-egg. However, for whatever reason, selection has favoured the second-laid B-egg in crested penguins. It being physiologically impossible to have a second egg without laying a first egg, the best the crested penguins can do is reduce investment in the first egg. Erect-crested penguins do this to an extreme extent and have the largest egg-size dimorphism of all penguins, indeed, all birds" (Davis et al 2022 p17).

"Migratory carry-over effects" (Crossin et al 2010) may explain the investment in the B-egg. This is the idea that the female body is not fully ready for egg-laying when first arriving after migration (eg: hormone levels). The risk of this has led to the smaller A-egg and the greater investment in the B-egg when the body should be fully ready (Davis et al 2022).

References

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5.2. FEMALE ROBINS SING

Vocal performance by many bird species is "almost entirely based on research on male song" (p194), in part because females were assumed not to sing (Dudouit et al 2022). Male song is viewed as a secondary sexual characteristic (ie: a means of signalling quality to the female), and is used in male-male competition, and territorial defence.

There are species where females sing, though the functions of such song are "not well understood" (Dudouit et al 2022 p194). Dudouit et al (2022) studied the European robin (Erithacus rubecula), where both males and females sing. During the breeding season, male-female pairs hold territories, while at other times, the birds have individual territories, and females sing at this time (Dudouit et al 2022).

Data were collected on twenty-two ring-identified robins at a university campus in France between October and December 2019. Songs were recorded and analysed. The birds of both sexes produced the same level of vocal performance (as measured by, for example, sound density - "the proportion of time dedicated to singing in a song as opposed to the time not singing"; Dudouit et al 2022 p195). "This suggests a similar function for female and male song outside the breeding season: to regulate territorial competitive interactions and social competition with members of either sex" (Dudouit et al 2022 p200).

The vocal performance, however, did not appear to convey information about the signaller's body size or body condition as there were no correlations between aspects of the song and body measures (eg: wing length). Male song in the breeding season is an honest signal where the differences in song convey information about differences in body size and condition of the singer.

The evolution of song in female robins seems to be linked to environmental conditions outside the breeding season. "During autumn and winter, resident European robins suffer from high energy demands and at the same time from a reduced number of available prey items... Furthermore, winter can be associated with higher vulnerability to predation pressure from Eurasian sparrowhawks, Accipiter nisus, for instance... The evolutionary response of European robins is to live in separate individual territories, used as food supply and safe shelter, the most important properties of territories for this species... Thus, the vocal performance of both sexes of European robins singing to deter male and female rivals should be equal..." (Dudouit et al 2022 p200).

Reference

Dudouit, C et al (2022) Vocal performance during spontaneous song is equal in male and female European robins Animal Behaviour 193, 193-203

5.3. FIRST MIGRATION

The initial urge to migrate in birds is inherited. For example, captive-bred European blackcaps have a preference for the direction of migration, while "young cuckoos, which grow as parasites in the nests of different species, know to migrate like other cuckoos, without having met any" (Sarchet 2022 p28).

But this is not the case for all migrating species, as in young Caspian terns, who are accompanied by their fathers on the first migration from Northern Europe to Africa. Birds that lost contact with the father during the migration died.

GPS devices have allowed the tracking of migrating birds, as in Byholm et al's (2022) study of thirty-one Caspian terns (Hydroprogne caspia) (figure 5.1) using data from 2016 to 2020. Nine young terns migrated with their father, one with a male foster parent, and one with their mother. Breeding partners did not migrate together.

(Source: Daderot; at Pacific Grove Museum of National History; public domain)

Figure 5.1 - Model of Caspian tern and chick.

It was found that four young birds that lost contact with their parent during the migration died. Also the birds in subsequent years "remained faithful to routes they took with their parents as young" (Byholm et al 2022 p1). This was based on using the same stopover sites as the first migration.

The role of the male parent here is important in terms of the fitness of the young (ie: it is "extended parental care"; Byholm et al 2022). The researchers classed the first migration together as an example of "teaching behaviour" by the father, which Byholm et al (2022) defined as "(1) the teacher modifies their behaviour in the presence of a naive observer, (2) there is a cost incurred by doing so, and (3) the teacher's modified behaviour leads the observer to acquire the behaviour faster or more efficiently than it might have done otherwise" (p4).

References

Byholm, B et al (2022) Paternal transmission of migration knowledge in a long-distance bird migrant Nature Communications 13, 1566

Sarchet, P (2022) Eternal sunshine New Scientist 19th November, p28

5.4. DIVORCE AMONG BIRDS

Though most bird species are socially monogamous, "divorce" does happen. This is described as "an individual re-mating with a new partner while its former partner of the last breeding season is still alive" (Chen et al 2022).

What causes divorce? Two main hypotheses have been proposed (Chen et al 2022):

i) Divorce is an adaptive strategy to increase reproductive fitness (ie: it produces novel genetic variation in offspring). This may be deliberate choice of another partner, choice of a new territory and partner also, or incompatibility between current partners ("active" explanation).

ii) Divorce is a consequence of events like the death of one partner, or an intruder takes over territory and partner, or migration ("passive" explanation).

Chen et al (2022) investigated these two explanations using a dataset of 232 avian species. The annual divorce rate (defined as "the percentage of pairs that both survived but changed mates from one year to the next year in a population"; Chen et al 2022) was calculated for monogamous pairs. A promiscuity score was also calculated for each species (based on number of reported observations of such behaviour in a species).

The researchers found that the divorce rate was not directly related to mortality of partner, but increased with male (but not female) promiscuity score, and was associated with longer migration distance. The latter finding "could be explained by asynchrony in migration, as longer migration might amplify the time-lag of arrival between partners and lead to a higher degree of asynchrony in arrival. Moreover, long-distance migration extends travel time and narrows the time window for breeding. In this context, divorce could be a salvage strategy to ensure breeding for the year when partner do not arrive with each other..." (Chen et al 2022).

The findings supported a combination of both hypotheses above.

Reference

Chen, Y et al (2022) Divorce rate in birds increases with male promiscuity and migration distance bioRxiv (https://www.biorxiv.org/content/10.1101/2022.10.13.512018v1)

5.5. HUMAN HARASSMENT

Intentional disturbance or harassment, like noise-making machines to scare birds around airports, are employed to manage wildlife in human-animal interactions. "For harassment to influence the behaviour of a targeted animal, animals must perceive harassment as a threat of injury or death. Animals generally respond to human disturbance as if it were a predation risk as many species have evolved with hunting by humans or have evolved responses to generalised predator behaviours such as direct approach" (Askren et al 2022 pp2-3).

Non-lethal harassment aims to increase the energetic cost of one site, and so encourage movement elsewhere. But animals may become habituated to the harassment, and/or the cost of moving elsewhere may be greater than the perceived risk at this site.

The Canada goose (Branta canadensis) in urban North America and Europe is a species where harassment has been tried. "Canada geese are associated with conflicts in urban areas including aggression towards people when nesting, faecal and feather deposition leading to decreased aesthetic values of greenspaces, and risks to air traffic" (Askren et al 2022 p3).

Askren et al (2022) studied the impact of harassment (with noise) on 47 Canada geese in Chicago fitted with GPS transmitters. The study periods were December 2017 - March 2018 and December 2018 - March 2019 (n = 627 harassment events observed).

Harassment during the winter in an urban park produced more time in flight and movement behaviours (than non-harassment areas), but "harassment resulted in short-term behavioural changes that may not have significantly affected energetic costs of using the site and did not accomplish the management goals of causing individuals to leave the area or avoid a specific location for more than 48 hours" (Askren et al 2022 p12). Weather was a stronger predictor of use of a particular site.

Reference

Askren, R.J et al (2022) Behavioural responses of Canada geese to winter harassment in the context of human-wildlife conflicts Wildlife Society Bulletin 46, e1384

5.6. INCUBATOR HEAT

Incubation temperature of eggs has an impact on later life. This has been studied in the controlled situation of commercial incubators with chickens. The standard temperature of 37.6 °C maximises hatchability, which is most important commercially. Studies have tested between 34.6 °C and 41 °C, for instance (Verlinden et al 2023).

In terms of future behaviours, Verlinden et al (2023) studied fearfulness, and sociality (amongst conspecifics and with humans). Three batches of eggs were compared - standard 37.6 °C (control group), 1 °C higher for some of the time, and 2 °C higher for part of the time.

After hatching, various behavioural tests were performed. For example, a novel object is placed in an arena and the chick's willingness to explore it is used as a measure of fearfulness, as well as the presence of a stationary or an approaching human. These behaviours were not effected by incubation temperature.

But the sociality of males did increase with incubation temperature. This was shown in more time with other chicks (in the "social zone") when given the choice, for example.

The researchers offered a potential evolutionary explanation for the findings: "In the wild, eggs will be challenged by fluctuating temperatures, both higher and lower than the standard temperature of 37.6 °C used in industry. The creation of a diverse nest, comprising birds with different levels of sociality, could potentially increase the survival rate of the nest in different natural environments. This phenomenon has been proposed before by Hepp and Kennamer (2012) who found incubation temperature (both warmer and colder) to influence later life reproductive success [in wood ducks in the wild in the USA]" (Verlinden et al 2023 p9).

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