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Comparative Psychology Stuff

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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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CONTENTS

1. RULES AND CHALLENGES

1.1. EVOLUTIONARY "RULES"

The understanding of evolution, particularly in the 19th century, led to a number of evolutionary "rules" being proposed (Barras 2023):

i) "Cope's rule" (after Edward Drinker Cope in the 19th century [1]) - Becoming a larger body size over evolutionary time is better. The assumption is that evolutionary advantages are associated with larger size (eg: reduced risk from predators).

Study: Heim et al (2015) compiled a data set of adult body sizes for over 17 000 genera of marine animals living and extinct in the last 542 million years. There was some evidence found for evolution towards larger body size over time. The mean biovolume had increased over time, but "most of the size increase reflects differential diversification across classes, indicating that the pattern does not reflect a simple scaling-up of widespread and persistent selection for larger size within populations" (Heim et al 2015 p867).

ii) "Allen's rule" (after Joel Asalph Allen in the 1870s) - The size of the appendages is linked to environmental temperature. It states that "animals with longer appendages (hence higher surface-area-to-volume ratio) are more likely to be found in hot climates, where shedding excess body heat may be needed. In turn, shorter appendages (lower surface-area-to-volume ratio) are more likely found in cold conditions, where effective retention of warmth is required" (Frohlich et al 2023 p1).

"Bergmann's rule" (from the 1840s) is often associated with Allen's rule, and it states that body size decreases in warm climates. This is because small

[1] Eg: Cope (1896).

body size (which produces a higher surface-area-to-volume ratio) results in more effective heat exchange with the ambient environment and hence is advantageous in warm conditions" (Frohlich et al 2023 p1).

Putting the two rules together, we should expect animals living at the equator to have small bodies with large appendages, and the opposite for those in polar regions.

Study: Frohlich et al (2023) examined the interaction of the rules in the case of birds (with data on 9962 species). The relative length of unfeathered appendages varied with temperature, but it depended on the overall body size. So, beak and tarsus (foot bones) length increased with temperature more in larger bodied species, while tarsus length decreased with temperature in smaller birds. The findings suggested an "evolutionary compromise" between the two rules (Frohlich et al 2023).

iii) "Foster's (or island) rule" (J.Bristol Foster 1964) - Large animal species isolated on islands become smaller, while small animal species become larger.

Put another way, gigantism in small animals and dwarfism in large animals on islands compared to mainland relatives. Explanations for the rule include reduced predation, relaxed competition, or resource limitations (Benitez-Lopez et al 2021).

Study: Comparing island and mainland relatives, Benitez-Lopez et al (2021) found support for the rule in mammals, birds, and reptiles, but not amphibians, which tended towards gigantism on islands only. The magnitude of change, however, was influenced by climate, island size, and degree of isolation, "with more pronounced effects in smaller, more remote islands for mammals and reptiles" (Benitez-Lopez et al 2021 p768).

Benitez-Lopez et al (2021) analysed a data set of 2479 island-mainland species of terrestrial vertebrates. A log response ratio was calculated between the mean body size of individuals from an island/insular population and from mainland relatives. So, a negative value indicated dwarfism and a positive value gigantism on islands. The researchers controlled for certain variables that influenced body size in their analysis, like water availability, and resource limitation.

iv) "Van Valen's law" (or law of constant extinction) (Van Valen 1973) - The length of the existence of a species does not lower the extinction risk (ie: ancient species are as likely as newer species to become extinct). Put another way, "the probability of extinction of a taxon during the next time interval does not depend on its age" (Zliobaite 2024 pp1-2).

Zliobaite (2024) observed: "No matter how well an individual is adapted, its close relative or even its own local descendant can be all the same but slightly better adapted for the current circumstances, and thus at any time give a rise to a new lineage without a need to start accumulating traits from scratch" (p2).

Leigh Van Valen initially described survivorship based on age, and found three possible relationships:

- Type I - "the probability of dying in the next time step accelerates with the individual's age" (Zliobaite 2024 p2).

- Type II - the probability of dying is the same for all ages.

- Type III - the probability of dying decreases with age.

The Type II relationship was applied to species extinction based on fossil records. If Type I was correct, extinction risk would increase with age of species, while younger species would have an increased extinction risk if Type III was correct (Zliobaite 2024).

v) "Gloger's rule" (Constantin Gloger in the 1830s) - Endothermic species have darker colours in warm/rainy climates. While the "complex Gloger's rule" (eg: Delhey 2017) predicts more rufous (redness) in warm/dry climates (Marcondes et al 2021).

Study: Marcondes et al (2021) analysed data on plumage colour for 250 Furnariid species (ovenbirds and woodcreepers). It was found that Gloger's rule was the result of various selection pressures (eg: crypsis; parasite deterrence; thermoregulation), such it was supported in some situations only.

Firstly, controlling for habitat type, birds in cooler and rainier climates had darker plumage, and birds in dark habitats had darker plumage (controlling for climate). "The effects of temperature and precipitation interact so that the negative effect of precipitation on brightness is strongest in cool temperatures" (Marcondes et al 2021 p592). Birds were more rufous in both warm/dry and cool/wet climates.

In summary, Gloger's rule was supported in relation to precipitation, but not temperature (Marcondes et al 2021).

1.2. CHALLENGES TO BIOLOGICAL LAWS

1.2.1. Obligate Chimerism

"A fundamental law of biological inheritance" in multi-cellular organisms is that a single zygote produced by a sperm and an egg is the basis to the genetics of all cells (ie: every cell has the same genes) (Darras et al 2023 p55). The yellow crazy ant (Anoplolepis gracilipes) (figure 1.1) has broken this law, according to a study by Darras et al (2023).

(Source: Philipp Hoenle; public domain)

Figure 1.1 - Yellow crazy ant.

Males are chimeras of two divergent lineages - R ("reproductive queen") and W ("worker"). R sperm fertilising an egg produces a queen, while W sperm leads to a worker as the offspring. "The most likely explanation was that workers developed from crosses between two divergent lineages, whereas queens arose from crosses between parents of the same lineage, a pattern described in a few other ant species" (Darras et al 2023 p55).

Genetic analyses of ants collected at fourteen locations in Asia showed that queens and workers were genetically quite different (eg: no shared alleles at 12 of 16 loci studied). It seems that queens inherit one copy of the R genome from each parent, while workers received the R genome from the mother and the W genome from the father.

"Obligate chimerism" was the term used to describe this inheritance process (Darras et al 2023). Chimerism has been observed occasionally in a wide range of animals. For example, chimerism (of a sort) has been reported in marmosets (eg: Ross et al 2007). "Females frequently give birth to dizygotic twins, which exchange stem cells in utero via their shared placenta. These exchanges lead to extensive chimerism in both the somatic tissues and germ lines of the adults. By contrast, chimerism in A. gracilipes is associated with a single fertilisation event at the onset of development" (Darras et al 2023 p58).

1.2.2. Becoming a Male

The SRY gene on the Y chromosome upregulates Sox9 expression in mammals that triggers testis development, but "there are a few exceptional rodent lineages in which the Y chromosome, and SRY have been lost. This means testis differentiation must proceed without SRY, and raises questions about the identity of the genetic trigger that can up-regulate Sox9 expression" (Terao et al 2022 p1).

One of the exceptions is the Amami (or Ryukyu) spiny rat (Tokudaia osimensis) (figure 1.2), which lacks a Y chromosome, and so no SRY gene (ie: both males and females have a single X chromosome). This animal is indigenous to a single island (Amami-Oshima island) in the Ryukyu archipelago, southern Japan. An alternative mechanism has evolved for signalling testis development (tiny changes in genes on chromosome 3).

The importance of Sox9 has been shown in transgenic mice with XX chromosomes (ie: female) that change males with the added SRY gene (Vidal et al 2001). While humans with disorders of sex development (DSD) have been found to have mutations in Sox9 coding (eg: Kim et al 2015).

(Source: Totti; public domain)

Figure 1.2 - Stuffed model of Amami spiny rat.

1.3. TINY FROGS

A number of species of tiny frogs have been discovered in recent years, of which the adults are smaller than 25 mm in length (Bolanos et al 2024). But which is the smallest?

Lehr and Coloma (2008), for example, proposed the Brazilian gold frog (Brachycephalus didactylus) with a snout-vent length (SVL) of 8 to 9 mm, out of a list of forty small frog species. While the New Guinea Amau frog (Paedophryne amauensis) was found at 7.7 mm average total length in Papua New Guinea (Rittmeyer et al 2012).

Bolanos et al (2024) put the case for the Brazilian flea toad (Brachycephalus pulex) with an average SVL of 7.10 mm for males (and 8,15 mm for females). These figures were based on specimens at a zoological museum in Brazil.

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2. AVOIDANCE LEARNING

2.1. ACTIVITY-BASED FLAVOUR AVOIDANCE LEARNING

"Activity-based flavour avoidance learning" describes the situation where animals "learn to avoid the flavoured substance consumed immediately before running in activity wheels or swimming in water buckets" (Nakajima et al 2023 p1).

Here is an example of an experiment using this phenomenon with laboratory mice (table 2.1) (Nakajima et al 2023) [2]. Individual mice were presented with new food (cheese or raisin) before a twenty-minute swimming activity (experimental condition) or not (control condition). When offered the new food subsequently less was consumed by the experimental than control condition mice. However, both groups increased their consumption over time with repeated presentations.

- Independent variable - Twenty-minute swimming activity or not after the eating the new food.
- Dependent variable - Amount of new food eaten after swimming activity (mg).
- Design - Independent groups (or unrelated or between-participants): Participants are involved in one condition only.
- Control of confounding variables - eg: housing conditions; availability of food.
- Potential confounder - Mice in the control condition immediately returned to their home cages. Subsequent experiments introduced a 20-minute confinement in a box while the experimental group was swimming.

Table 2.1 - Key aspects of the experimental method as used by Nakajima et al (2023).

It is proposed that (undesirable) activity after eating produces nausea, which becomes associated with the

[2] This was Experiment 1 of seven reported by Nakajima et al (2023).

food, and this is the reason that the animals avoid the food. This is negative classical conditioning or avoidance learning.

It should be noted that activity-based flavour avoidance learning has been studied more in laboratory rats (eg: Masaki and Nakajima 2004) than laboratory mice, and it is more common in the former. "In laboratory rats, flavoured solutions are typically employed as targets for avoidance learning. Although it is not impossible to demonstrate running-based avoidance of flavoured solutions in mice..., mice do not drink much in absolute values, making it difficult to accurately measure intake given some spillage during bottle presentation of the solution" (Nakajima et al 2023 p1).

2.2. CONDITIONED TASTE AVERSION

Domestic livestock are attractive to carnivores, and this livestock depredation produces human-carnivore conflict. One possible solution is conditioned taste aversion (CTA) - ie: to teach the carnivore an association of a specific food with illness. Gustavson et al (1974) first showed this with coyotes attacking domestic sheep. Meat baits containing lithium chloride were left around for coyotes to consume. Further studies have supported the success of CTA, but there are confounders (eg: detection of lithium chloride before eating meat the first time), which mean CTA is not always effective (Cassaigne et al 2023).

"Meat baits designed to produce CTA in predators must contain an appropriate dose of a substance that safely and effectively induces a temporary gastro-enteric discomfort, in the same manner as a food-borne illness. Many substances are known to induce an aversion, but few have the combination of safety, effectiveness, and most importantly, a low detectability that is required when used with predators" (Cassaigne et al 2023 p2).

Thiabendazole (TBZ) is another possible chemical to use. Cassaigne et al (2023) tested the effectiveness of TBZ in CTA with six captive jaguars in Mexico. Meat baits covered in the skin of domestic livestock and treated with TBZ were given to the animals. CTA was created after one eating and lasted for at least thirty days (ie: the jaguars avoided subsequent meat baits).

Cassaigne et al (2023) then captured two free-ranging jaguars known to kill calves and dogs and tested them. These animals "displayed a spatial avoidance after being treated" (Cassaigne et al 2023 p1).

Invasive cane toads in Australia are toxic to freshwater crocodiles, for instance, and they have severely impacted the latter's numbers (Ward-Fear et al 2024). Could CTA work here?

A number of laboratory and small-scale field studies have used this method to discourage eating of the toads (eg: Price-Rees et al 2013). These studies have established proof of principle. Ward-Fear et al (2024) reported a larger study of CTA with crocodiles in the Kimberley region of north-west Australia.

"Cane toads (Rhinella marina; formerly Bufo marinus) are large bufonids that were introduced into Australia as a biocontrol agent in 1935. They failed at their original purpose, but have spread throughout tropical Australia. The toads are highly toxic and exude powerful cardio-toxins from the parotid glands when threatened. Most Australian predators lack evolutionary history with bufonids (and their associated bufotoxins), and die within minutes of trying to consume a cane toad" (Ward-Fear et al 2024 p2).

In September and October 2021 baits were left out for the crocodiles. These were dead adult cane toads with the toxic organs removed and injected with lithium chloride to cause nausea. Chicken baits without the chemical were the controls. Each trial took place over five days, and in total, around 2400 baits were used.

The proportion of baits taken declined from Day 1 (mean 92%) to Day 5 (51%). This suggested CTA was working.

Crocodile mortality from consuming cane toads was lower in bait areas than control areas. Ward-Fear et al (2024) were positive about the results: "our study suggests that a relatively simple management intervention (deployment of taste-aversion-inducing baits) can buffer populations of free-living crocodiles from catastrophic decline due to invasive cane toads. In our study system with a novel toxic species, taste aversion training is best applied immediately prior to the arrival of the invasion, with the aim of curtailing the inevitable wave of predator mortality as the toads move through a new area" (p11).

2.3. AVERSIVE GEOFENCING

More generally, aversive conditioning is the association of an unwanted behaviour with an unpleasant stimulus, as in "virtual fencing". This is the use of electronic training collars ("shock collars"), which are activated when an animal moves into or out of a certain area. It has been used to keep coyotes, wolves, and dingoes, for example, out of certain areas, and to keep livestock and domestic dogs within areas (Cabral del Mel et al 2023b).

Aversive geofencing devices (AGDs) make use of satellite tracking to automatically deliver warning sounds followed by an electric shock when an animal crosses a virtual boundary. "The advantage of AGDs is that as the animal learns to associate the warning sound with the electric shock, they can predict and avoid receiving the electric shock... In other words, animals can control the receipt of electric shocks, thereby reducing the anxiety and stress caused to themselves... and thus minimise the welfare impact of AGDs on their well-being" (Cabral de Mel et al 2023b p2).

Reducing human-animal conflict is one possibility with AGDs, as in Asian elephants in Sri Lanka. Cabral de Mel et al (2023a and b) studied this with captive elephants. Cabral de Mel et al (2023a) showed that elephants learned to avoid receiving the electric shock, while Cabral de Mel et al (2023b) studied the welfare impacts on the animals.

Two pilot experiments with eight captive elephants at an elephant orphanage in Sri Lanka showed increased stress at the beginning of training (ie: the first few electric shocks), but this settled down with learning (Cabral de Mel et al 2023b).

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3. SOCIAL PREDATION

Appendix 3A - Dangerous prey
Appendix 3B - Automated behaviour analysis

Predators may be solitary hunters and/or work together (social predation) (or co-operative hunting or foraging). The latter is particularly useful with dangerous prey (appendix 3A) and a high risk of injury. It can "release species from physiological and competitive constraints" (Twining and Mills 2021 p1) (table 3.1). But Herbert-Read et al (2016) pointed out that "individuals do not necessarily increase the amount of prey they consume when hunting together (compared with when hunting alone)" (p2) (eg: food intake per wolf; Schmidt and Mech 1997). On the other hand, black-headed gulls captured twice as many fishes when hunting as groups of six than when hunting as an individual (Gotmark et al 1986).

STRENGTHS	WEAKNESSES
1. Easier to find food as more searchers involved, and so travel less distance. 2. Reduces risk of injury or death when faced with dangerous prey. 3. Can hunt larger prey than when alone. 4. Better for attacking smaller grouping prey. 5. Releases animal from individual constraints (eg: physiological). 6. Better for protecting kill from kleptoparasites and competitors. 7. General advantages of groups like increased vigilance, and learn from observing others.	1. Groups easier to spot for prey. 2. Problems of predators (that do not live together all the time) finding each other, organising and co-ordinating attacks. 3. Too many predators attacking at same time risk injuring each other. 4. Sharing of food, and potential conflicts. 5. In some cases, it does not increase the amount of prey consumed compared to lone hunting. 6. Risk of "free rider" who does less work compared to others, and/or waits until prey is weakened by other predators before attacking themselves. 7. General disadvantages of groups like increased pathogen transmission.

Table 3.1 - Key strengths and weaknesses of social predation.

"Social predation includes a suite of behaviours that encompasses the species' degree of sociality and dependence on social foraging as well as its communication, specialisation, and resource sharing... These different traits can be found in various combinations depending on the species. Complex social predation strategies, which include choreographed attack patterns, are used by animals that live socially... as well as by animals that are generally solitary... Some species are able to subdue or consume their prey in a way that is more efficient as a result of their collective actions, for example electric eels sometimes herd and surround their prey and then subdue large numbers with joint electrical strikes... and lionfish which have increased success during hunting when multiple individuals attack the same group, but do not show co-ordination... This framework also encompasses more simple forms of social predation characterised by aggregation, such as that of brown bears who live solitarily, but aggregate at food sources..., and predatory nematode-hunting mites that aggregate around injured prey... Aggregation as a strategy differs from other strategies in that the individuals are feeding together but their behaviours are largely independent of one another" (Otter et al 2024 p3).

Herbert-Read et al (2016) used the term "proto-co-operation" to describe unco-ordinated, alternating attacks by individuals, as these researchers observed with sailfish (Istiophorus platyterus) attacking schooling sardine in the Gulf of Mexico [3]. They explained: "When hunters attack smaller grouping prey, the reasons for group hunting appear clearer. In some cases, group hunters use their superior speed and co-ordinated attacks to disrupt and fragment prey groups. Groups of piscivorous fishes, for example, have a higher probability of breaking up prey schools and capture more prey than single attackers" (Herbert-Read et al 2016 p2).

Herbert-Read et al (2016) summed up their findings: "While only 24% of attacks result in prey capture, multiple prey are injured in 95% of attacks, resulting in an increase of injured fish in the school with the number of attacks. How quickly prey are captured is positively correlated with the level of injury of the school, suggesting that hunters can benefit from other conspecifics' attacks on the prey" (p1).

[3] Studies like this involve human researchers in many hours of observation in difficult environments. There is great hope that artificial intelligence-based systems can be an alternative (appendix 3B).

Some species show individual and social predation. Twining and Mills (2021) reported the opportunistic observation of co-operative foraging by wild yellow-throated martens (Martes flavigula) (figure 3.1) in India. The two adults alternatively attempted and succeeded to subdue and kill a (larger than them) macaque. "The martens (Martes sp) have been used as examples of obligately solitary species, physiologically and morphologically restricted by their inability to store fat and specialisation in homogeneously distributed small vertebrate prey, and therefore presumed incapable of advanced social behaviours" (Twining and Mills 2021 p1). The changing climate and resources "may release the species from typical constraints associated with martens" (Twining and Mills 2021 p1).

(Source: Altaipanther; public domain)

Figure 3.1 - Yellow-Throated Marten in a zoo.

Hunting groups can occasionally involve different species working together, like the usually solitary big blue or day octopus (Octopus cyanea) and various fish species (eg: long barbel goatfish; blacktip grouper) (Sampaio et al 2024). These researchers filmed thirteen group hunting scenes from 120 hours of diving off the coast of Israel in 2018-2019.

The fish benefitted from the association as "the octopus serves as a specialist that they can guide to specific locations to produce prey otherwise unattainable. For the octopus, fish (in particular goatfish) act as an 'extended sensorial system' that samples larger spatial areas of the environment at a faster rate than the octopus could via direct sensing" (Sampaio et al 2024 p2079).

The researchers argued for a functional complexity in octopus-fish hunting not seen in other mixed species hunting groups (eg: badger-coyote; Thornton et al 2018).

APPENDIX 3A - DANGEROUS PREY

"Predators have more at stake while hunting than simply the risk of missing a meal if unsuccessful. Some potential prey may harm or even kill their predator, or the habitat in which particular prey are found may pose an injury or mortality risk to a predator" (Mukherjee and Heithaus 2013 p551). Mukherjee and Heithaus (2013) reviewed the decisions and factors in attacking dangerous prey.

Prey can be dangerous for physical, chemical and/or behavioural reasons. For example, weapons like spines, teeth, and tusks are physical defences, while noxious chemicals can be used to deter or injure predators. Behavioural factors can include counter-attacks, like kicking and biting, or making the risk higher for predators. For example: "In deep-sea habitats, consuming bioluminescent prey can increase the chances of a predator being attacked by their own predators" (Mukherjee and Heithaus 2013 p551). Characteristics of the habitat can add to the danger (eg: Nubian ibex take shelter on steep cliff faces; Mukherjee and Heithaus 2013).

The frequency of injury inflicted by prey is difficult to say generally, but there are specific studies. For example, Murza et al (2000) found that 6% of American kestrels in Canada had hunting-related injuries (eg: broken toes, talons or flight feathers), while around 5% of lions and 10% of leopards, for instance, had injuries in other studies (Mukherjee and Heithaus 2013).

Predators can reduce such risks by not hunting dangerous prey when there is a choice, or using a different strategy (eg: orb-web spiders grab non-venomous prey, but use a web to subdue dangerous prey) (Mukherjee and Heithaus 2013). Minimising contact or handling time is another strategy, or attacking a certain area (eg: lizard predators attack lizard prey on the head and neck to avoid being bitten) (Mukherjee and Heithaus 2013).

The trade-off between costs and benefits in hunting dangerous prey includes factors like individual differences in willingness to take risks, experience, and foraging ability, and differences in body condition, and availability of social predation, as well as prey availability and abundance (Mukherjee and Heithaus 2013).

Mukherjee and Heithaus (2013) presented a decision-making model for choice of prey based on total time spent hunting a prey, and number of attempts or attacks needed to succeed (table 3.2).

		TOTAL TIME SPENT HUNTING	
		LOW	HIGH
NUMBER OF ATTEMPTS OR ATTACKS TO SUCCEED	LOW	Least dangerous and easiest to hunt	A long period of stalking, say, but easily killed when found (eg: snow leopard and blue sheep in the Himalayas)
	HIGH	A prey that can escape, when finally caught can be killed quickly (eg: cheetahs and Thompson's gazelles)	Most dangerous: "Many attempts are needed because the predator has to catch and release its prey several times in order to avoid physical injury" (Mukherjee and Heithaus 2013 p558)

(Based on Mukherjee and Heithaus 2013 figure 4 p558)

Table 3.2 - A decision model of prey choice.

APPENDIX 3B - AUTOMATED BEHAVIOUR ANALYSIS

"Automated behaviour analysis" (ABA) is the use of computers to process information about animals. As Siegford et al (2023) hoped: "There is growing optimism that soon, ethologists will not have to manually decode hours (and hours) of animal behaviour videos, but that instead a computer can process visual, audiological, and other animal-based information for scientists working to gain insight into animal lives" (p2). But the researchers were also realistic about ABA (also called "computational ethology" (Anderson and Perona 2014) or "computational analysis of behaviour" (Egnor and Branson 2016)).

One particular hope for ABA is the collection of large amounts of data, possibly continuously and in real time, and for many individual animals. Siegford et al (2023) noted nearly 25 000 peer-reviewed publications on the subject.

These researchers stated that "before we assume ABA is ready for practical use, it is important to take a realistic look at exactly what ABA is being developed, the expertise being used to develop it, and the context in which these studies occur. Once we understand common pitfalls occurring during ABA development and identify limitations, we can construct robust ABA tools to achieve automated (ultimately even continuous and real time) analysis of behavioural data, allowing for more detailed or longer-term studies of behaviour on larger numbers of animals than ever before. ABA is only as good as it is trained to be" (Siegford et al 2023 p1).

A key issue is the data set for training algorithms. They are often relatively small and "lack sufficient variability in animal morphometrics, activities, camera viewpoints, and environmental features to be generalisable. Thus, ABA often needs to be further validated before being used satisfactorily on different populations or under other conditions, even for research purposes" (Siegford et al 2023 p1).

Reference data sets is one solution, which could be used for benchmarking. Agreed standards for such data sets are important, as well as the actual collection and sharing of such information.

Siegford et al (2023) outlined some crucial questions for the humans behind the ABA, including:

a) "How well do the humans training the ABA understand the behaviour they are attempting to monitor?" (p4).

b) "Do they understand the specific postures or actions that make up the functional behaviour?" (p4).

c) "If they try to interpret motivations or meanings underlying the behaviour, are these in line with the scientific research on these behaviours?" (p5).

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4. SPIDERS

4.1. NUTRIENT-SPECIFIC FORAGING SPIDERS

Food is required to stop hunger, but the content of the diet (eg: macronutrients) is also important. Generalist foragers achieve the balanced diet by feeding on a variety of resources, while specialist foragers may have to supplement their intake some way. "Nutrient-specific foraging" is the term used, and it includes the selection of specific prey [4].

Cuff et al (2025) studied generalists in the form of money spiders and wolf spiders captured in fields at a farm in south Wales. Three hundred spiders were captured in 2018. The gut contents of the spiders were analysed for specific nutrients.

There was a great variety in the different proportions of carbohydrate and protein in the prey consumed, as well as sex differences; "specifically, the diets of male spiders included prey that were more carbohydrate-rich on average, while the diets of females included more protein-rich prey" (Cuff et al 2025 p5).

Statistically significant deviations from random foraging were found, which suggested prey choice. A statistical "null diet" was created which assumed random consumption of prey and three macronutrients (protein, carbohydrate, and lipid), and the actual diet was compared to this to see if it was significantly different (ie: expected by chance vs observed diets).

So, selective foraging for prey rich in the three macronutrients was evident, though this varied between species, life stage, and sex of spider. This could be taken as nutrient-specific foraging, but the researchers accepted that it was impossible to be certain. Most invertebrate studies on the subject have been controlled laboratory feeding trials, "in part because of the technical challenges of studying invertebrate diets in nature... The disparity in results between lab and field

[4] "While nutrient-specific foraging can occur at any stage of predation, from the selection of specific prey to the extraction of certain nutrients from specific tissues..., evidence identifies selection of specific prey as the primary means" (Cuff et al 2025 p2).

studies of invertebrate nutrition confounds comparison of these data and the application of lab-based findings to natural systems" (Cuff et al 2025 p2).

4.2. PIRATE SPIDERS

Spider webs have evolved in a variety of ways from the basic web design, including "a silk line immersed in a sphere of liquid silk that the spider throws on males of some moth species", while jumping spiders, for example, have "abandoned the cost of trap webs" (Barrantes et al 2025 p1). The type of web is linked to the prey capture strategy.

Barrantes et al (2025) described a novel example by a species of "pirate spider" (Gelanor siquirres) which attack other spiders. Observations were made in Costa Rica in 2016. This spider produces a web that is a series of silk lines attached to the underside of leaves and then retreats. "If an exploring spider attaches its floating line to the silk line of the pirate spider's web, then the exploring spider walks along its line to the pirate spider's line. As the pirate spider perceives the exploring spider on its web, it descends from the retreat and attacks the exploring spider" (Barrantes et al 2025 p1).

Put simply, the lines of the G.siquirres become part of the web construction of the prey spider, and oblivious to this fact the prey spider wanders around what it thinks is its web until it is near enough to be attacked. The G.siquirres' strategy has evolved to exploit the web building behaviour of the orb weaver (prey), for example.

"Pirate spiders" generally creep on to the web of the prey spider and slowly move towards the centre to capture them.

4.3. INDIVIDUAL RECOGNITION BY A SPIDER

Individual recognition (or "individuation of conspecifics"; Bonatti et al 2002) is assumed to require a larger brain, and to be a product of social animals. Dahl and Cheng (2024) found an exception in an asocial and miniature-brained jumping spider (Phidippus regius) (figure 4.1) (commonly called the regal jumper).

The researchers used a habituation-dishabituation procedure. This is, Dahl and Cheng (2024) explained, "where, in general terms, one individual habituates to the presence of another individual in its close proximity and dishabituates when, after a short phase of visual separation, another individual is present in close proximity, assuming that the one individual is capable of discriminating the identities of the two individuals it was confronted with. In other terms, with this habituation-dishabituation paradigm we expect to see that the rebound in 'interest' following changes in a spider's identity is greater than the rebound in 'interest' following a repetition of identity" (p2). If there is no recognition of an individual, then the spider will behave the same when presented with the same or a different individual.

For example, individual A and individual B were exposed to each other for seven minutes, then there was a three-minute gap before individual A was exposed to individual B (habituation trial) or individual C (dishabituation trial) for seven minutes. "Interest" was operationalised as the distance between the individuals (ie: high interest = shorter distance). Each of 36 spiders was exposed to six trials in three sessions. Overall, the distance in the dishabituation trials was significantly shorter than in habituation trials.

This jumping spiders appears to recognise individuals of its own species. In social animals individual recognition is important in relation to territoriality, aggressive competition, and parental care, but what is the biological relevance of this ability to the regal jumper, asked Dahl and Cheng (2024). They offered this possible explanation: "One of the few social instances in the life of a jumping spider occurs during reproductive communication, encompassing a complex visual courtship display of co-ordinated movement patterns of the body and bodily features. It is believed that the typical colouration of the appendages (Chelicerae) and the colouration and facial hair characteristics serve as important features for species and sex classification in jumping spiders and as a general indicator about the quality of an individual as a mating partner. Hence, colouration (sender) and the ability to distinguish certain colours (receiver) seem to be sufficiently beneficial to sexual selection" (Dahl and Cheng 2024 p5). So, the neural development for this type of recognition includes individual recognition (ie: it is related to the spider's general learning capabilities). This is known as the "generalised learning hypothesis" (Wiley 2013). Dahl and Cheng (2024) stated that "while for social animal species, including social arthropod species, there is an ultimate explanation addressing the function (or adaptation) of individual recognition, we cannot conclusively infer the survival benefits gained by individual recognition in P.regius. Instead we put forward the idea that individual recognition in P.regius is a byproduct of fairly sophisticated cognitive processing capabilities" (p6).

(Source: spidereyes2020; public domain)

Figure 4.1 - A male regal jumper.

4.4. MANIPULATIVE SPIDERS

Sedentary predators can use signals to draw prey to them. An interesting example is the orb-weaving spider Araneus ventricosus that uses flashing signals to draw in the firefly Abscondita terminalis. The signals are produced by a male caught in the web who broadcasts the flashes typically made by females in order for the spider to capture more male fireflies.

How does the spider get the male to mimic the female signals? Fu et al (2024) speculated that "spider deployed a specialised prey-handling procedure based on repeated wrap-bite attacks... Further research is needed to determine whether it is the spider's venom or its act of biting that exerts the manipulating effect on flashing" (pR768).

In their experiment, the researchers showed that the spider had to be present on the web for the male firefly to produce the female signals. In other conditions, this did not happen - (i) the male firefly on the web, but no spider present; (ii) the firefly's "lantern" blackened out (and spider present); and (iii) a control condition (no firefly or spider on the web). The capture rate of fireflies was used as the dependent variable. In total, 161 webs were involved.

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5. INSECTS

5.1. CAFFEINE AND ANTS

Invasive ant species, like Argentine ants (Linepithema humile), "can outcompete native ants, leading to declines in biodiversity and abundance, which in turn, can have a variety of direct and indirect effects on other non-ant species" (Galante et al 2024 p1).

This species is a "central place forager", which means that ants travel out from the nest to seek food sources and bring back home their finds. Navigation is influenced by path integration, and learnt information.

"Path integration combines compass information with an odometer to continuously track the ant's position relative to a reference point, usually either the nest or a frequently visited feeding site. This global vector allows ants to return back to the reference point even when navigating through featureless and novel environments. Simultaneously, many insects also employ view-based navigation. They are able to take a panoramic snapshot of a goal, such as their nest, a food source, or a point along a path and later compare it with their current view. Importantly, view-based navigation differs from path integration in that it does not exclusively rely on idiothetic cues. Instead, it is grounded in an individual's ability to perceive and learn environmental cues" (Galante et al 2024 p1).

Caffeine impacts memory and learning. Galante et al (2024) gave 142 Argentine ants different concentrations of caffeine in an open landscape foraging experiment. Under low and intermediate caffeine concentrations (25 and 250 ppm caffeine in water respectively) the ants were 38% faster with each consecutive visit to reach the food reward (ie: paths became straighter with each visit to the known area - "foodward path optimisation") compared to the no-caffeine control. This improvement was lost with high concentrations of caffeine (2000 parts per million; ppm) , and caffeine overall had no effect on average speed with each visit to known place or homing behaviour (ie: nestward journey). Generally, caffeine boosted learning and memory.

So, if the ants took 300 seconds to find the food on the initial visit, in the control condition, it took 252 seconds on the third visit. The latter figure was 113 seconds in the low caffeine dose condition, 54 seconds intermediate dose, and 273 seconds high dose.

5.2. FLYING EXCRETA

The millimetre-sized glassy-winged sharpshooter (GWSS) (Homalodisca vitripennis) (figure 5.1) is a xylem-feeding insect. This diet (95% water) is nutrient-deficient, meaning that the GWSS is energetically constrained. Excretion is energetically costly to pump out due to negative tension. For "these tiny insects, the super-propulsion of droplets is energetically cheaper than forming jets, enabling them to survive on an extreme energy-constrained xylem-sap diet" (Challita et al 2023 p1).

Super-propulsion is "a phenomenon in which an elastic projectile can achieve higher velocity than the underlying actuator through temporal tuning" (Challita et al 2023 p1). High-speed filming of 22 events by 5 GWSS showed three phases to the process - droplet formation, spring loading, and droplet ejection. A rotating "anal stylus" is key to the final phases (Challita et al 2023).

Flinging droplets large distances also reduces the risk of detection by predators, like parasitic wasps, which may respond to chemical cues in the accumulation of GWSS excretion (Challita et al 2023).

"The need to create a considerable distance between insects and their waste is mainly observed in shelter-dwelling or site-faithful insects, which are typically pressured to maintain hygiene at the site to avoid the growth of pathogens and reduce chemical cues for potential predators. The ballistic ejection of excrement is not uncommon among insects. Many insect species may be described as 'frass-shooters', 'butt-flickers', and 'turd-hurlers' [Weiss 2006] that innovated unusual strategies to launch away both liquid and solid excrements. For instance, frass-shooting skipper larvae employ biological latches on their anal plates coupled with a hydrostatic blood pressure build-up to propel solid pellets up to 38 times their body length with a speed larger than 1.5 m/s. Some species of noctuids violently shake their abdomen as they release their frass pellets, and some geometrid larvae use their thoracic legs to kick away their frass pellets" (Challita et al 2023 p7).

(Source: "Insects Unlocked" project at University of Texas at Austin; public domain)

Figure 5.1 - Glassy-winged sharpshooter.

5.3. EATING FAECES

Bacteria living on or in another organism in a joint beneficial relationship is mutualism or symbiosis. It occurs often through vertical symbiont transmission (ie: from parent to offspring).

But there is also horizontal transmission, which occurs with the squash bug Anasa tristis (DeGeer) and its microbial symbiont Caballeronia. This is "where adults produce symbiont-free offspring that must acquire their mutualistic bacteria from the environment. This strategy is inherently risky, as some nymphs may not find the symbionts they need or may accidentally acquire a less beneficial strain" (Villa et al 2023 p2830).

One way that offspring A.tristis acquire the bacteria is through finding and eating adult squash bug faeces. Experiments showed nymphs flocking to the faeces just deposited by an adult. In over 200 forced choice trials (ie: faeces or sterile substance), 99% of the time nymphs chose the faeces. Even when the faeces had been treated to kill the bacteria, nymphs still preferred it to a control substance. Nymphs also showed searching behaviour when deprived of access to the bacteria, while nymphs satisfied did not wander.

5.4. FLIGHT-TO-LIGHT AND ARTIFICIAL LIGHT

"Artificial light at night" (ALAN), particularly as in urban areas, affects insects by altering their day-night cycles, and changing where they go (ie: attracted or repelled by light).

ALAN can be seen as a selection pressure. For example, Altermatt and Ebert (2016) found that spindle ermine moths (Yponomeuta cagnagella) reared in urban light conditions had a 30% weaker flight-to-light response than those reared in rural areas. "Altermatt & Ebert [2016] discussed two mutually non-exclusive mechanisms explaining the observed patterns: first, a decreased perception of light; and second, a reduced overall mobility in urban moths, which could also result from a (non-adaptive) by-product of selection on other traits" (Van de Schoot et al 2024 p2).

Van de Schoot et al's (2024) follow-up experiment found support for the latter explanation. Moth larvae collected in Switzerland and France were used in this study (as in Altermatt and Ebert 2016). "Urban individuals were found to have on average smaller wings than rural moths, which in turn correlated with a lower probability of being attracted to an artificial light source" (Van de Schoot et al 2024 p1).

These researchers accepted that they had not controlled for changes in eye morphology of urban moths and other physiological changes (Van de Schoot et al 2024).

5.5. WING-SLAPPING ANTI-PREDATOR DEFENCE

Eusocial organisms live in large groups, which include adults, eggs, and larvae. This is attractive to predators, and eusocial organisms have developed specific defensive behaviours. For example, honey bees respond to predatory hornets with the use of "shimmering waves" and "defensive balling" (Seko et al 2024).

Seko et al (2024) reported a specific defensive behaviour by the Japanese honey bee (Apis cerana japonica) against the Japanese pavement ant (Tetramorium tsushimae). The behaviour is "wing-slapping" - the ants are repelled from the hive entrance by the bees placing their wings in contact with ants and flicking them away. This direct contact is different, because of the risk of injury or death, and previously it was observed that bees fanned their wings to blow the ants away (eg: Yang et al 2010).

Filming Japanese honey bee colonies, Seko et al (2024) introduced various ant species to the vicinity of the hive entrance. The researchers observed that "whereas wing-slapping had a success rate of roughly one in two or three attempts in repelling intruding Japanese queenless ants and Japanese pavement ants, the success rate against Japanese wood ants was relatively low, suggesting the behaviour might not be effective against all ant species. Given that Japanese wood ants have about twice the body length and move more quickly than the other species examined in the present study, it may have been difficult to successfully flick them away" (Seko et al 2024 p4).

Note that Japanese queenless ants and Japanese pavement ants "rarely bite and consume healthy workers in the hive... Therefore, in Japan, where predator ants such as the Asian weaver ant are absent and the threat of direct predation by ants is low, non-contact defensive behaviours might not always be optimal. In other words, ants with low direct predation threat can be eliminated more efficiently (ie: with lower energy cost) through direct contact rather than through generating wind pressure" (Seko et al 2024 p4).

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6. OCEAN LIFE

6.1. POP-OFF SATELLITE ARCHIVAL TAGS

"Pop-off satellite archival tags" (PSATs) are used with different marine species. Anderson et al (2024) described their use with a species of shark called a porbeagle (Lamna nasus) (figure 6.1). Individuals were caught off Massachusetts, USA, in 2020 and 2022 by rod-and-reel, examined on the boat, and a PSAT was attached through a hole in the first dorsal fin. The PSAT was set to release after one year and float to the sea surface to be collected by the researchers. Water temperature and depth (pressure in dbar) were recorded every twenty seconds, as well as geolocation.

Sometimes the individuals with PSATs die, either from and soon after the capture and tagging experience, or by predation. The latter can be established (ie: tag ingested by a predator) by data changes including temperature increases (ie: the stomach temperature of the predator) or depth alterations (Anderson et al 2024).

(Source: NMFS, E.Hoffmayer, S.Iglesias, and R.McAuley; public domain)

Figure 6.1 - Porbeagle.

Anderson et al (2024) reported the first evidence of predation of a porbeagle with a tagged pregnant female in the Northwest Atlantic. "Predation was evident approximately 5 months after tagging based on depth and temperature data transmitted by the PSAT. Four days prior to PSAT pop-off, depth data indicated that the tag continued to descend and ascend in the water column while the temperature remained approximately 5 °C above ambient levels, even at several hundred metres in depth, indicating ingestion. Given the location of predation and elevated temperature at depth recorded by the pregnant porbeagle's tag, potential predators include endothermic shark species such as the white shark Carcharodon carcharias and shortfin mako Isurus oxyrhinchus" (Anderson et al 2024 p1).

6.2. BREACHING BEHAVIOUR

Breaching behaviour is where an underwater animal propels themselves out of the water and into the air, landing on the sea surface, and displacing water upon contact. Sometimes the animal does not fully clear the water. This behaviour has been shown by elasmobranch fishes (sharks and rays), but why?

"Given the energetic investment required for these large-bodied fishes to propel themselves out of the water..., there are likely adaptive fitness or survival benefits" (Klimley et al 2025 p442).

Klimley et al (2025) reviewed the literature around ten possible functions of the behaviour: "(1) parasite removal, (2) clearing of gill rakers, (3) expulsion of faeces or internal parasites, (4) courtship, (5) attraction of conspecifics, (6) repelled by conspecifics and interspecifics, (7) evasion by conspecifics, (8) feeding, (9) concentrating or stunning of prey, and (10) birthing" (p441). Breaching was defined as "any leap in which at least four tenths of the animal's body rises above the water" (Klimley et al 2025 p442).

The researchers concluded that there was no single function of the behaviour, and the reason varied between species. The ten possible explanations could be summarised in order of number of species reported - cleaning (1-3) (eg: 19 species and external parasite removal), feeding (8-9), communication (4-6), evasion (7), and birthing (10).

6.3. SELF-AWARE CLEANER FISH

Self-awareness in non-humans is measured by the "mirror self-recognition" (MSR) test (ie: the ability to recognise the reflection as oneself). Often a mark is put surreptitiously on the animal's body that can only be seen in the mirror to see if an attempt is made to touch or remove the mark. Great apes, dolphins, and elephants, for example, had passed the MSR test (Kobayashi et al 2024).

But the level of self-awareness of such animals is questioned. "Self-awareness is categorised into two classes based on the nature of self-information being processed. The fundamental level is called public self-awareness, which enables individuals to focus on perceptual self-aspects observable by others, such as behaviour or appearance. Private self-awareness, which represents a more sophisticated level, allows individuals to focus on their internal aspects; that is, mental states, such as mental images, goals, self-memories, perceptions, intentions, and standards. Some researchers regard MSR as an indicator of public self-awareness and object to the inclusion of private self-awareness in its interpretation" (Kobayashi et al 2024 p1).

Kobayashi et al (2024) investigated private self-awareness in the cleaner wrasse fish (Labroides dimidiatus) using kinaesthetic visual matching. In situations of potential conflict, fish swim parallel to assess the body size of the rival to their own. Cleaner fish had previously been found to show public self-awareness in the MSR test (eg: Kohda et al 2019).

Kobayashi et al (2024) argued that if cleaner fish have private self-awareness, they will be able to use the information about their body size in the mirror (ie: maintain a mental image) in future interactions with rivals. Fifteen wild fish were presented with full size photographs of rivals larger or smaller than themselves after viewing themselves in the mirror or not. Three photographs were used - same body size as viewer, 10% larger, and 10% smaller.

The fish showed the same amount of aggression to all three photographs without the mirror, but "exhibited less aggression toward the larger and same-sized photographs compared to the smaller ones after attaining MSR. Together with the control treatment, the findings indicate that mirror-experienced fish may reduce their aggression not merely due to habituation to the photographs presented twice but rather by improving their ability to discriminate 10% size differences between themselves and the photograph by attaining MSR" (Kobayashi et al 2024 p5). This suggested a mental image of themselves attained from the mirror, and potential evidence for private self-awareness.

Why cleaner fish might have such abilities relates to their environment and social behaviour. Kobayashi et al (2024) explained: "Males establish their harems, which include several females, and a strict size-dependent dominance hierarchy maintains social relationships among individuals. In particular, females of similar body sizes have exclusive territories, whereas those of different body sizes occasionally overlap in their territorial boundaries. Cleaner fish primarily feed on ectoparasites or mucus on the surface of client fish that visit their territories. Therefore, defending their territory against conspecific rivals of similar size is essential for their survival. They have approximately 2,300 daily interactions with more than 100 species and can discriminate between individual clients. Such complex social interactions are considered to develop various sophisticated cognitive capacities in addition to MSR, such as tactical deception, and transitive inference. They also provide rudimentary evidence of episodic-like memory and theory of mind" (p6) (table 6.1).

STUDY	COGNITIVE ABILITY
Bshary (2002)	Tactical deception
Hotta et al (2020)	Transitive inference
McAuliffe et al (2021)	Theory of mind

Table 6.1 - Studies showing sophisticated cognitive abilities of cleaner fish.

6.4. OCTOPUS HAS NIGHTMARES?

Ramos et al (2023) reported a case study (table 6.2) of a male Brazilian reef octopus (Octopus insularis) (figure 6.2) that showed unusual sleep behaviours. it is known that during "active sleep" octopuses generally "display sequences of camouflage patterns and modulation of basal rhythms, while remaining relatively unresponsive to outside stimuli. Some scientists have speculated that these states could be analogous to dreaming in mammals, involving episodic recall with a narrative structure" (Ramos et al 2023 p1).

STRENGTHS	WEAKNESSES
1. An opportunity to study rare, unusual, or abnormal behaviour not usually seen in the majority of the population or observed before. 2. Provides information to prompt further research and hypotheses. 3. Detailed study of a small number of individuals or a single individual more than is possible to study with many participants.	1. Generalisation to the whole population not possible as no way of knowing how representative the case(s) are. 2. May distract from the behaviour of the majority of the population. 3. Quantitative analysis limited as there are a small number of data points.

Table 6.2 - Key strengths and weaknesses of the case study method.

Video monitoring of the case over a month recorded four brief episodes (between 44 and 290 seconds in length) in which "the octopus abruptly emerged from quiescent or active sleep, detached itself from its sleep position, and engaged in anti-predator and predatory behaviours (with no predator present). The longest of these episodes resembled the species-typical response to a predatory attack, suggesting that the animal may have been responding to a negative episodic memory or exhibiting a form of parasomnia" (Ramos et al 2023 p1).

It was speculated that the behaviour was similar to a nightmare (ie: the traumatic recall of previous predator attacks during sleep). The male octopus was kept in a laboratory environment, and the "first three episodes occurred within the first few weeks of its acclimation to the new environment, a period in which the animal often displayed anti-predator body displays and increased arousal in response to the novel laboratory environment. These episodes could be the result of a naturally heightened arousal of octopuses during sleep in response to novel sensory stimuli. Alternatively, it is possible that an imbalance in its light/dark cycle relative to its previous environment in the wild, or imbalances in oxygenation of its tank increased the likelihood of sleep disturbances. However, at this stage this assertion is largely speculative" (Ramos et al 2023 pp10-11).

(Source: Andra Waagmeester; public domain)

Figure 6.2 - A Brazilian reef octopus.

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7. IRIDESCENCE AS AN ANTI-PREDATOR STRATEGY

"Iridescence is a striking form of structural colouration in which hue and intensity vary with the angle of view or illumination" (Kjernsmo et al 2022 p45). It may have evolved as a form of camouflage, or as another anti-predator strategy - aposematism ("signalling unprofitability") (Kjernsmo et al 2022). For example, Waldron et al (2017) found that a species of iridescent leaf beetle that had chemical defences produced avoidance learning in birds with an increase in specular reflection (gloss).

Avoidance learning by predators during their lifetime means a cost to some prey and some predators, but the evolution of avoidance learning from birth is the ideal. This can be tested with naive predators, as Kjernsmo et al (2022) did.

Naive chicks of domestic fowl were presented with real or artificial jewel beetle (Sternocera aequisinata) wing cases (which varied in level of gloss and iridescence) with an edible, dead, mealworm partially sticking out. Thirty-two chicks performed all four conditions in randomised order (table 7.1).

Iridescence (hue and intensity vary with angle of viewing)	Specular reflection (gloss): High/glossy	Specular reflection (gloss): Low/matte
High	GI (glossy iridescent)	MI (matte iridescent)
Low (static spectrum)	GS (glossy static spectrum)	MS (matte static spectrum)

Table 7.1 - Four conditions of the experiment by Kjernsmo et al (2022).

Willingness to attack (ie: peak at) was significantly reduced by iridescence. An average of half the number of attacks in the GI and MI conditions as in the GS and MS conditions. The researchers explained: "Considering that all birds in our experiment were naive, any behavioural response they showed in their first prey encounter can be considered unlearnt. Interestingly, the birds initially hesitated to attack the iridescent, but not the static spectrum prey: having multiple colours displayed at the same time is not enough to elicit aversion. Rather, it is the key feature of iridescence, its colour changeability, that is important for this protective effect" (Kjernsmo et al 2022 pp48-49).

BACKGROUND MATCHING

Crypsis through background matching can be an effective anti-predator strategy. The animal regulates their body colour to match the background of their habitat. But some animals live in changing environments (both over time and geographically), so the ability to change colour is important.

"Colour change is a remarkable form of phenotypic plasticity and can occur at varying rates, from changes in seasonal phenotypes to near instantaneous shifts. Its function for improving crypsis has been documented in a broad range of taxa, spanning multiple classes of both aquatic and terrestrial vertebrates and invertebrates, from reptiles, mammals and birds to cephalopods and arthropods. However, its underlying mechanisms and the selective pressures driving the evolution of pigmentation plasticity are complex and not yet well understood. Although slow colour change seems to be more common, our knowledge on the sensitivity of pigmentation plasticity and its associated physiological costs are largely restricted to a few organisms, typically those that can change colour rapidly" (Liedtke et al 2023 p1). Note that plasticity incurs costs for the animal.

Liedtke et al (2023) studied the tadpoles of the western spadefoot toad (Pelobates cultripes) (figure 7.1) that live for up to six months in waterbodies with seasonal changing vegetation (in Spain, in this case). In experiments, tadpoles were reared in water with different backgrounds - black, white, red, or blue - and five shades of grey (to assess different brightness) for 60 days. Some tadpoles had their background changed in the middle of the experiment.

It was found that tadpoles could "regulate pigmentation to track fine-grained differences in background brightness, but not hue or saturation" (Liedtke et al 2023 p1). Skin pigement change was rapid and reversible (though darkening of skin was faster than lightening), and was achieved by the quantity of eumelanin in the skin.

Furthermore, the researchers found that "increased eumelanin production and/or maintenance is also correlated with changes in morphology and oxidative stress, with more pigmented tadpoles growing larger tail fins and having an improved redox status [oxidation state]” (Liedtke et al 2023 p1).

It appears that “the same, or components of the same, hormonal pathways” are involved in colour change and body development (Liedtke et al 2023 p8).

(Source: David Delon; public domain)

Figure 7.1 - Young western spadefoot toad.

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8. BIRDS

8.1. FORAGING ENRICHMENT

It has been suggested that parrots have "an intrinsic motivation to put effort in acquiring and handling food items..., which can – at least in part – be explained by their diet, ecology and evolution... The granivorous diet of most parrots requires a high degree of (time-consuming) exploration and manipulation of food items with the beak, tongue and feet, so-called podomandibulation" (Beekmans et al 2023 p1). This is often not satisfied in captive situations. Wild parrots spend 4-8 hours per day foraging compared to less than one hour per day for captive parrots (Beekmans et al 2023).

So, "foraging enrichment" is recommended for captive parrots to avoid the development of abnormal and repetitive behaviours like feather damaging. Forging enrichment involves "items and toys that stimulate the bird to search, procure, extract or process food" (Beekmans et al 2023 p2). Such enrichment needs to satiate appetitive (exploration, search and procurement of food) and consummatory (manipulation, selection and consumption of food) phases of foraging (Beekmans et al 2023).

Beekmans et al (2023) studied a new foraging enrichment with grey parrots (Psittacus erithacus). Twelve adults housed at a research facility in the Netherlands were used. The experiment involved four conditions - appetitive enrichment (APP), consummatory enrichment (CONS), both (APP+CONS), and control/no enrichment. The APP involved an automated device requiring the following action sequence: "1) pick up a marble from the food trough; 2) transport the marble to the opening of the marble track; 3) put the marble in the marble track; 4) manipulate three levers with the beak (respectively rotate, lift and pull) to remove obstacles from the marble track that hindered free passage of the marble; 5) walk/climb towards the food trough and wait for deliverance of food; and 6) search, select, and eat out of the marble-filled trough. After the third obstacle, the marble would pass an optic sensor which activated a food dispenser, and fell into the food trough together with the food and other marbles" (Beekmans et al 2023 p3). The CONS had cardboard capsules containing food that needed to be opened. There were 7-14 days of acclimatisation, and thirty days of testing. Measures, including daily time spent on foraging behaviour, and amount of food consumed, were taken.

In the control condition, the average time spent on foraging behaviour was 121 minutes per 24 hours, but there was significantly more in the other conditions - 176 (APP), 194 (CONS), and 234 minutes (APP+CONS). Males spent longer foraging than females. Food consumption was highest in the CONS condition. The study showed the benefits of providing foraging enrichment to captive parrots.

The time spent in foraging was higher in this research than in similar studies - eg: 123 minutes (grey parrots; van Zeeland et al 2013); 185 minutes (Orange-winged Amazon parrots; Rozek et al 2010).

8.2. FREE-RANGE HENS

"Access to an outdoor range offers laying hens improved opportunities to perform natural behaviours and increases available foraging materials... In addition, range use can effectively reduce stocking density within the house, potentially contributing to improved environmental and social conditions" (Wurtz et al 2023 p1). But individuals vary in their use of an outdoor range.

There is a correlation between range use and health of the hen. Note that this is a two-way relationship, as in the example of foot health. "Foot health may be impacted by conditions within the house (eg: litter moisture or house temperature) or on the range (eg: standing water or faeces accumulation)... On the other hand, hens with foot disorders may be less motivated to explore the outdoors due to discomfort. Similarly, keel bone damage may impact a hens' mobility, and thus range access, and vice versa" (Wurtz et al 2023 p2).

Wurtz et al (2023) undertook an experiment with 120 hens randomly chosen from pens at poultry experimental facilities in Denmark. Two commercial hybrid lines were involved - "Dekalb White" and "Bovans Brown". The hens were given access to an open range, and data were collected over twenty weeks. The time spent in the open and indoors was recorded by observations and video monitoring. Regular welfare assessments were made. The individual level of fear was measured by the tonic immobility test (ie: handling that causes the hen to become immobile, and how long before they move again). Fearful individuals take longer to move again [5].

"Extent of range use was not associated with clinical welfare indicators nor fear levels as assessed by a tonic immobility test" (Wurtz et al 2023 p1). But greater range use did lead to better health (eg: more developed crop and gizzard), which may have been due to eating more forage.

The researchers admitted: "The lack of observed associations between clinical welfare indicators and range use may be in part due to the relatively young age that hens were at the end of the study" (Wurtz et al 2023 p8) (38 weeks old).

8.2.1. Spatial Complexity

Hens allowed to roam require "appropriate spatial skills to reduce the risk of injury... and ensure the successful locating of resources" (Rentsch et al 2023 p1). The first few weeks of life are crucial for developing such skills.

Rentsch et al (2023) varied the spatial complexity of the early environment in their experimental work. The participants were four flocks of "Lohmann Brown-lites" (browns) and "Lohmann Selected Leghorn-lites" (whites) strains. The flocks were kept in conventional cages, or lower, intermediate, or high complexity spatial environments (ie: differences in elevated perches and platforms) for the first six weeks of life. A T-maze was used as the testing environment at Week 4. Chicks were given five trials to locate a reward.

Those chicks kept in high and intermediate complexity environments performed best on the T-maze test, but there were differences between the genetic strains (figure 8.1). "In conclusion, laying hen spatial

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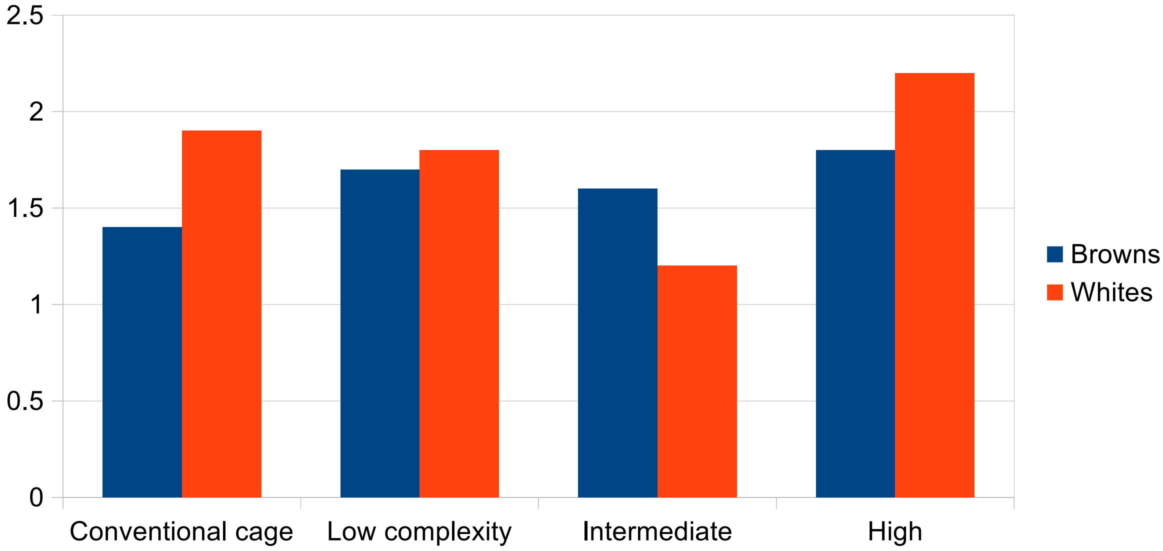
[5] Neuhauser et al (2023) commented: "Telomere shortening, a cellular biomarker of biological age, is a potential animal welfare indicator... Telomeres are repetitive sequences of DNA at the end of chromosomes that shorten with each cell division... In humans, negative life experiences result in shorter telomeres... and stress-related telomere shortening may decelerate by positive experiences... Thus, telomere shortening can be used as a biomarker of welfare in humans. Importantly, telomeres shorten faster in people with higher perceived stress..., showing the significance of affective states on telomere length. Similarly, in non-human animals (including domestic chickens...,telomeres shorten faster due to negative experience" (p2). However, these researchers found that hens housed in enriched environments who undertook fear assessment experiments did not show telomere shortening.

skills appeared to be sensitive to the degree of early life complexity as well as genetic strain" (Rentsch et al 2023 p1).



(Data from Rentsch et al 2023 table 1)

Figure 8.1 - Average number of correct choices in five T-maze trials based on early environment and genetic strain.

8.3. BOUBA-KIKI EFFECT

The "Bouba-Kiki effect" (Ramachandran and Hubbard 2001) describes an example of "sound symbolism", where the non-word "Kiki" is imagined as a spiky object, and "Bouba" as a round one.

Sound symbolism is the "connection between a meaningless arbitrary sound and a likewise meaningless geometrical shape..." (Loconsole et al 2024 p1). Kohler (1947) had first noted the association of non-word "Maluma" with a round object, and "Takete" with a spiky object.

Sound symbolism (or "sound-shape cross-modal correspondences") has been found in pre-verbal human infants (eg: four months-olds; Ozturk et al 2013). Some researchers argued that the Bouba-Kiki effect is an example of "a predisposed perceptual mechanism at the basis of language acquisition, facilitating vocabulary construction and communication in infancy" (Loconsole et al 2024 p2). But others countered that "studies on infants are not conclusive, as they could not completely rule out a fast experience-driven origin of the effect resulting from infants' speed of learning, their high sensitivity to environmental statistical regularities, and the large number of symbolic associations of sounds to which they are exposed when interacting with adults" (Loconsole et al 2024 p2).

Studies with non-humans would suggest an evolutionary basis to sound symbolism. "This mechanism could confer an advantage to the individuals, allowing them to make accurate predictions about co-occurrences in the environment, reducing uncertainty, and allowing the formation of coherent and meaningful representations of objects and events, such as facilitating certain associations (eg: small objects and high pitch sounds, or small objects and elevated spatial positions) while hindering those that are less frequent. Sound symbolism, namely, the Bouba-Kiki effect, may constitute one of these shared cross-modal representations" (Loconsole et al 2024 p2).

Loconsole et al (2024) studied the Bouba-Kiki effect in naive newborn domestic chicks. Forty-two three day-old chicks learned to reach food rewards in panels with a spiky or round shape while Bouba or Kiki were played over a loudspeaker. Then in 24 test trials, the chicks were given a choice of panels while one of the two sounds was played. "Chicks preferred the panel with the spiky shape when hearing the 'Kiki' sound, and that with the round shape when hearing the 'Bouba' sound" (Loconsole et al 2024 p1).

8.4. BARN SWALLOWS

The barn swallow (Hirundo rustica) breeds across the whole Northern Hemisphere, but there are differences in male sexual signalling traits between sub-species (table 8.1) (eg: melanin-based ventral colour; tail streamer length) (Schield et al 2024).

- Hirundo rustica rustica
- H r savignil
- H r transitiva
- H r tyleri
- H r gutturalis
- H r erythrogaster

Table 8.1 - Six sub-species of barn swallow in the Northern Hemisphere.

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9. RIBOSOMES

Ribosomes are "sites of protein synthesis" within each cell (Aspden et al 2025) [6]. Initially (in the 1950s), it was believed that each ribosome specialised in synthesising a single protein, but subsequently, the prevailing view came to be that "ribosomes are non-specialised structures that synthesise different proteins depending on the mRNA they contain" (Aspden et al 2025 p1). Though ribosome specialisation has become popular again in the 21st century (Aspden et al 2025) [7] [8].

Aspden et al (2025) saw these changes in the views on ribosomes as "a reflection of a broader philosophical tension in biology: the struggle between reductionism and emergent complexity. The early view of ribosomes as uniform molecular machines aligned with the reductionist framework that dominated mid-twentieth century molecular biology — a time when the central dogma of gene expression was being solidified. In this model, the ribosome was merely a passive conduit for genetic information, faithfully translating mRNA into protein without bias or specialisation. This perspective offered a comforting simplicity, reducing the complexity of life to a set of uniform, predictable biochemical processes. However, as history has shown time and again, nature resists oversimplification. The emerging evidence of ribosome heterogeneity challenges this mechanistic view, forcing a shift toward a more dynamic, systems-level understanding of translation and gene regulation" (pp1-2).

They continued that "the ribosome embodies the philosophical concept of plasticity — its form and function are not fixed but instead adapt to the physiological and developmental needs of the organism. This mirrors the broader theme in biology that identity is not static but context-dependent, a principle seen in stem cell differentiation, neural plasticity and even ecological adaptation.
The discovery that ribosomes are specialized, that they selectively translate different mRNAs in different tissues and developmental stages, suggests that life is

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[6] Ribosomes are involved in gene expression in the translation of mRNA into proteins, and it is a "tightly controlled step" (Beaven et al 2025 p1). "The ribosome is a multi-sub-unit complex normally composed of approximately 80 ribosomal proteins (RPs) and four rRNAs (five in Drosophila melanogaster)" (Beaven et al 2025 p2).

[7] Beaven et al (2025) stated: "While there are numerous examples of heterogenous ribosomes, there are comparatively few bona fide specialised ribosomes described" (p1).

[8] "Deletion of genes encoding specific ribosomal proteins has revealed that heterogeneity in the ribosome must exist in vertebrate..." (Moser et al 2025 p1).

not merely governed by a universal set of molecular rules but is instead sculpted by intricate regulatory networks that respond to the needs of the organism. This recognition moves us away from the deterministic idea that genes alone dictate biological outcomes, and toward a more holistic view in which the cell, the tissue and even the ribosome contribute to the final expression of genetic potential. Ribosome specialisation, then, is not just a molecular mechanism — it is a reflection of life's ability to fine-tune itself, to carve out specificity and meaning from what was once thought to be uniform and universal" (Aspden et al 2025 p2).

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