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Some More Animal Topics

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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. TO STAY OR GO

1.1. DISPERSAL - CHOICE AND FORCED

1.1.1. Coercive Female Transfer

Should individuals born in a social group stay when adults or disperse to another group? "Philopatry (staying within the natal social group or geographical area) is often advantageous, because philopatric animals avoid the many potential costs of dispersal... Dispersing animals suffer increased mortality..., are usually unfamiliar with the new area... and lose proximity to kin and social bonds" (Ekanayake-Weber and Swedell 2021 p267).

Female primates are more likely to be philopatric because of shared childcare, and, in some cases (eg: baboons), "having maternal kin (mothers, maternal sisters, daughters) in the group is crucial in attaining high dominance ranks" (Ekanayake-Weber and Swedell 2021 p267).

Dispersal, however, avoids inbreeding, and improves the reproductive/gene opportunities. Many animals show "co-dispersal" or "parallel dispersal" where a coalition of brothers, say, may leave together (eg: lions).

"Most hypotheses concerning dispersal assume that individuals behave somewhat optimally in response to the potential costs and benefits. However, dispersal is not always at the discretion of the disperser. For example, females are aggressively ejected from groups by same-sex competitors in some primate species, including red-fronted lemurs, Eulemur rufifrons, rhesus macaques, Macaca mulatta, and red howler monkeys, Alouatta seniculus... In hamadryas baboons, Papio hamadryas, females have even less control over dispersal, because they are coercively transferred by males among social units, a process that breaks up any social and kin bonds that may have been in place in the natal unit"

(Ekanayake-Weber and Swedell 2021 p268).

Among hamadryas baboons a male creates a group with a number of females (known as the "one-male unit"; OMU). Coercive transfer of females into an OMU can occur in four ways (Ekanayake-Weber and Swedell 2021):

i) Death of the leader of the OMU allows other males to opportunistically take females.

ii) A single male takes a single female from her natal group to start their own OMU.

iii) A male who is connected to an OMU "inherits" the females at the death of the leader.

iv) Direct challenge to the leader by another male.

But females may have some influence on the process. Ekanayake-Weber and Swedell (2021) used data from Ethiopia in a computer modelling study, which suggested that there is a combination of male and female behaviour involved in coercive transfer.

1.1.2. Bachelor Groups

In certain species where there is a dominant breeding male with a number of females, adolescent males are evicted from their natal group and form "bachelor groups". Sometimes bachelor groups form because all the females die or leave (environmental disruption explanation), or males choose to leave their natal group (individual choice explanation) (Kanyile et al 2021).

Kanyile et al (2021) explored these explanations with African striped mice (or four-striped grass mice) (Rhabdomys pumilio) in South Africa. Monthly data were collected (almost without fail) between January 2008 and December 2019 (covering thirteen generations) at the "Succulent Karoo Research Station" at the "Goegap Nature Reserve" in the Northern Cape Province. Marking of individual animals with a dye made identification of natal groups possible (of which 11-16 groups were monitored).

Bachelor males were assigned to one of two categories:

i) "Kin bachelors" - all females disappeared from a natal group leaving related individuals together.

ii) "Unrelated bachelors".

There was a third category initially, of related males who left their natal group and formed their own bachelor group, but this was only observed once, and so this category was subsumed into "kin bachelors".

Forty bachelor groups were observed, of which 56% were kin bachelor groups. Kin bachelor groups were more common during the non-breeding season, and the largest males left to breed. Non-breeding males remained together until the next breeding season. "Thus, these groups were formed not by individual male choice, but by the disappearance of all females, and they existed until males chose to disperse and switch to another tactic" (Kanyile et al 2021 p140).

Unrelated bachelor groups were short-lived during the breeding season, and after increasing their body mass males left to be "solitary roamers" or to form a breeding group. "This indicates that non-kin bachelors might represent an alternative reproductive tactic that is similar to roaming males, but with the advantage of social thermoregulation by huddling in a nest at night, which is known to be an important mechanism for reducing energy expenditure in this species" (Kanyile et al 2021 p140).

Note that body mass (ie: heavier or larger) is key to reproductive opportunities as a male defends a territory containing two to four breeding females. "Thus, body mass is important for territory defence as well as for the maintenance of social and reproductive tactics... Non-kin bachelors may thus be seen as males that are large enough to disperse, possibly due to the pressures of within-group reproductive competition..., but not competitive enough to obtain and defend a territory. This is common in many species, where forming bachelor groups is a tactic employed by less competitive males which may be excluded by territorial or resident males... These bachelor males form coalitions while they wait to secure a reproductive position in a group... or while they wait to gain a territory" (Kanyile et al 2021 p141).

The researchers did not have data on reproductive success, so it was not possible to say if unrelated bachelor groups was an alternative reproductive tactic in a situation of dominant males breeding with multiple females. But some males did choose to leave their natal group and to become solitary roamers (ie: looking for breeding opportunities), and in between formed bachelor groups to improve survival. Some males did stay in their natal groups and their reproductive success was "extremely low" (Kanyile et al 2021 p142).

1.2. BREEDING DISPERSAL

"Breeding dispersal" is "the movement of adults between successive breeding locations" (p31), and it is not easy to study because "individuals can be difficult to track over successive breeding periods and, in some species, breeding dispersal happens infrequently" (Fuirst et al 2021 p31).

Based on the literature, a number of variables are known to influence breeding dispersal, including (Fuirst et al 2021):

i) Site choice and territory - eg: leaving low-quality territory.

ii) Mate loss - moving to a new site after loss of previous mate.

iii) Age - eg: younger individuals evicted by older dominant ones.

iv) Sex bias - females are more likely to disperse as males invest more in territory holding.

v) Intra-specific competition - eg: males moving to avoid high levels of male-male competition.

vi) Population density - eg: more dispersal at low density because of mate shortage.

Long-term data are helpful, and Fuirst et al (2021) reported a period of 55 years on Canada jays (Perisoreus canadensis) in Algonquin Provincial Park, Ontario, Canada. The data covered 530 breeding adults and 2477 breeding events between 1964 and 2019. This bird is monogamous, and occupies permanent territories where food is cached for overwinter survival.

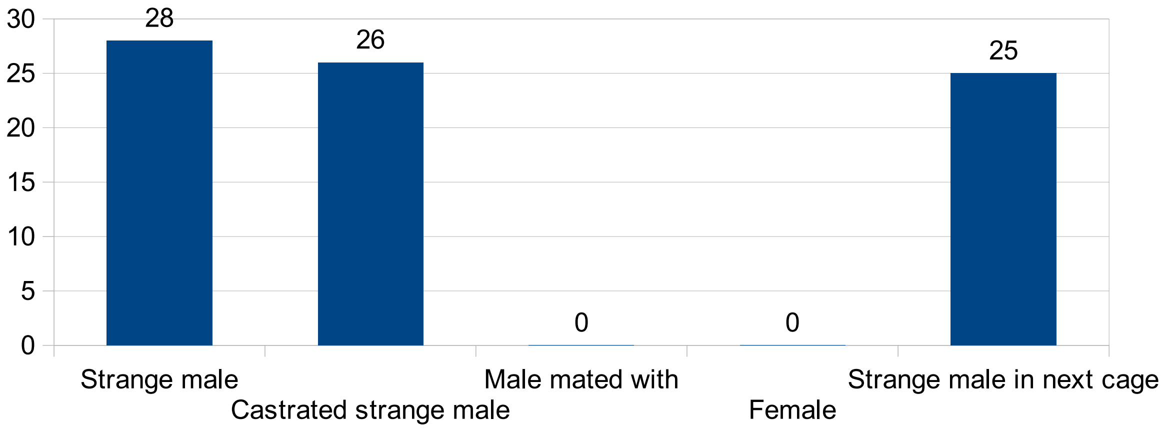
Overall, 13% of adults showed breeding dispersal at least once in their lifetime. So, the researchers concluded that breeding dispersal was low, and Fuirst et al (2021) suggested that this was because "overwintering Canada jays are critically dependent on the memory-accessed food items that they themselves cache on their territories during the summer and autumn. This constraint against abandoning their own cache-filled territories is supported by the fact that 70% of dispersers only moved to a neighbouring territory. Although we have no direct evidence, such short local breeding dispersal distances possibly allows individuals to retrieve food that was cached on their originating territory" (p37).

Loss of a mate occurred on 12% of occasions, but only 12% of these led to breeding dispersal. This occurred most in years of population decline (1982-1995), "suggesting that a diminishing pool of matte replacements influenced breeding dispersal decisions" (Fuirst et al 2021 p31).

Altogether, it seems that Canada jays moved only if forced by lack of new mates, and preferred not to because of the investment in their territory.

1.3. BRUCE EFFECT

The "Bruce effect" is where the presence of a strange male inhibits pregnancy in the female. It was first observed in experiments in rats (Bruce 1959). A female rat is allowed to mate, then placed in the vicinity of a strange male. "Pregnancy was blocked and implantation inhibited in nearly 30 per cent of females by the introduction of a strange male within 24 hr. of coitus; it was so blocked even by the presence of a castrated male. Pregnancy was not affected by the return of the female to her original stud male or by the presence of a strange female, whether parous or ovariectomised. Contact between the sexes was not necessary for this effect" (Bruce 1959 p105) (figure 1.1).



(Data from table 1 p105 Bruce 1959)

Figure 1.1 - Female rats having blocked pregnancy based on cage mate (%).

1.4. SITE FIDELITY

"Site fidelity" refers to the individual animal foraging in the same place on different occasions. There is great variety in this behaviour, and "all animals probably shift at least occasionally to other foraging sites in response to intrinsic or extrinsic drivers" (Bonnet-Lebrun et al 2021 p145).

The "win-stay-lose-shift" (WSLS) strategy has been proposed to explain site fidelity. "Under this strategy, an individual returns to its most recent foraging area only if the previous visit was successful (eg: total meal mass, or net energy gain per unit time, was high) but changes to a new foraging area if the last foraging visit was unsuccessful..." (Bonnet-Lebrun et al 2021 p145). An alternative is the "win-shift" strategy, where the individual changes site if the previous visit was successful. For example, nectar-feeding hummingbirds that deplete a flower's nectar at one visit (Bonnet-Lebrun et al 2021). So, time is needed for the food source to be replenished.

Soke animals pay no attention to past outcomes, as shown, for example, by Guitar et al (2017) in "a population of black-capped chickadees, Poecile atricapillus, where each individual used its own stereotyped search sequence of visits and revisits, irrespective of past outcome... They could also rely on a longer history of past successes and failures at a site rather than just the most recent visit as stated in the win-stay-lose-shift strategy" (Bonnet-Lebrun et al 2021 p146).

Foraging strategy has been studied in controlled experiments with captive or domestic animals (eg: pigs; Laughlin and Mendl 2000), but there is limited research in the wild.

Bonnet-Lebrun et al (2021) reported data on the black-browed albatross (Thalassarche melanophris) at Bird Island, South Georgia in 2002. Both parents take turns in foraging for fish to feed the chick at the nest. Six male and six female parents were fitted with satellite trackers. Data were available on 235 trips in terms of distance, and meal mass delivered to the chick.

There was weak support for the WSLS strategy - ie: "some evidence of a positive correlation between recent foraging success and probability of return to the same place. Moreover, returning to the area visited on a previously profitable trip provided a higher payoff than switching to a new foraging area, suggesting that this strategy had adaptive value in this environment" (Bonnet-

Lebrun et al 2021 p148). These researchers noted that the WSLS strategy may not be adapted wholeheartedly because of "more dynamic and heterogeneous oceanographic conditions and greater unpredictability of prey for black-browed albatrosses around South Georgia than other locations" (Bonnet-Lebrun et al 2021 p148). Also the chick is being fed by a dual foraging strategy (ie: both parents together), which is different to an individual animal deciding in relation to feeding themselves.

Foraging success (ie: meal mass) was calculated by weighing the chicks before and after feeding.

Discussing the theory of foraging strategies, Bonnet-Lebrun et al (2021) made this point: "In the wild, environmental conditions can change rapidly, the meal mass or profitability on one visit may be an imperfect indication of future reward (prey abundance or availability) and individuals may have to account for factors such as locomotory costs (eg: wind conditions), competitors and allocation trade-offs (self-maintenance versus offspring provisioning; exploration versus exploitation)" (p149).

Finally, they said: "To understand the conditions that drive the use of this [WSLS] strategy, further studies combining data on sites used in consecutive trips with indices of foraging success, for example using accelerometers, stomach temperature probes, beak sensors or other devices to quantify prey capture, or concurrent indices of prey availability, would be highly informative" (Bonnet-Lebrun et al 2021 p149).

1.4.1. Individual Foraging Specialisation

Individual foraging specialisation refers to “an individual whose niche is substantially narrower than that of its population, for reasons not attributable to its sex, age or discrete morphological group” (Sheppard et al 2021 p286). Living in a group can involve fierce competition for food resources, and so selection could favour a specialisation that reduces such intra-group conflict.

One example of foraging specialisation is improved foraging efficiency. For example, sea otters that focused on specific prey processed 25% more prey items than more generalist individuals (Tinker et al 2008).

1.5. RECOGNITION OF NESTMATES

Large insect colonies have a division of labour, where the majority of individuals are non-reproductive workers and a few are the reproductive caste (eg: queen). There is also the soldier caste in ants and termites, who defend the nest.

Recognition of nestmates from non-nestmates is crucial, particularly for soldiers. Bos and van Zweden (2021) studied this in the fungus-growing termite Macrotermes natalensis. Soldiers and workers were collected in South Africa from six different colonies for the experiments.

Two individuals were placed together and their behaviour was categorised - fleeing, aggression, or no response. All individuals responded significantly more to non-nestmates, with workers fleeing, but soldiers becoming aggressive. Workers were "less efficient at recognising and discriminating against conspecific non-nestmates than soldiers" (Bos and van Zweden 2021 p129). This suggested that soldiers have adapted to be more sensitive to "outsiders".

However, soldiers only responded aggressively to non-nestmates in some of the trials (20%). The researchers interpreted this finding thus: "it appears that fungus-growing termites are much less territorial or aggressive towards conspecifics than many other superorganismal insects..., which could be because they never parasitise or predate each other, and therefore do not encounter invading members of their own species" (Bos and van Zweden 2021 p129). There is thus no selection pressure to evolve highly sensitive odour and recognition systems specific to a nest.

1.6. FEMALE-FEMALE CONFLICT

Parents behave differently towards others during periods of parental care than in non-care phases. Bose et al (2021) studied this behaviour in a shell-dwelling African cichlid fish (Neolamprologus multifasciatus) in Lake Tanganyika. In groups of around twenty individuals, there is a dominant male and up to five adult females who lay eggs inside the shells.

During October 2018 twenty groups were observed, of which twelve had females raising offspring and eight groups with no offspring. Video recordings were analysed for aggressive and submissive behaviours in 30-minute intervals.

Female to female conflict was significantly higher in groups with offspring than not, while the male to male behaviour did not vary between groups. Where there was conflict, the dominant male would intervene and limit any potential escalation of aggression. This male "peace-keeping" behaviour has been reported before in this species (Schradin and Lamprecht 2000). Where dominant males were aggressive towards females, it was towards non-caregiving females rather than caregivers, "a bias that would suggest an effort by the males to minimise costs suffered by females as they care for dependent offspring" (Bose et al 2021 p99).

This study showed that the social behaviour of the group changed with the presence of dependent offspring. Bose et al (2021) explained: "Maternal aggression, or increases in female aggression when pregnant, gravid or in the presence of their offspring, has been documented in a wide variety of taxa and is likely to have evolved in response to threats posed by conspecifics... As in other closely related cichlid species such as N. pulcher..., N. multifasciatus females may pose threats to each other's offspring" (p97).

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2. EVOLUTIONARY GAME THEORY

2.1. 50 YEARS ON

Richter and Lehtonen (2023) described "evolutionary game theory" as "one of the great leaps forward since Darwin's insight" (p1). In particular, it provides a framework for understanding evolution in situations and populations than are not static. "Game theory can therefore be used to solve problems where the pay-off for adopting a given strategy depends on the strategies adopted by others, and there is no obvious 'best thing' for an individual to do. This underlying idea applies whether the focus is on economic behaviour in humans, or on evolution in populations of organisms that do not necessarily have the capacity for rational thinking" (Richter and Lehtonen 2023 p1).

Note that game theory was originally developed to explain economic behaviour, and Maynard Smith and Price (1973) is viewed as the "birth" of evolutionary game theory (Richter and Lehtonen 2023) [1] [2]. "The article of Maynard Smith and Price was largely motivated by the prevalence of 'limited war' conflicts in nature. Why do fights in nature not more commonly escalate far enough to result in serious injury or death?" (Richter and Lehtonen 2023 p1). With computer simulation, the idea became the "Hawk-Dove game" (Maynard Smith and Parker 1976), where the concept of the "evolutionarily stable strategy" (ESS) is important [3]. Hawks always attack and Doves always flee, and so a population equilibrium is achieved (ie: not all Hawks or not all Doves) (figure 2.1). Maynard Smith (1982) asserted that an ESS (denoted as "I") "must have the property that, if almost all members of the population adopt I, then the fitness of these typical members is greater than that of any possible mutant; otherwise, the mutant could invade the population, and I would not be stable" (quoted in Richter and Lehtonen

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[1] Technically, Maynard Smith and Price (1973) was not the first use of game theory in biology, Fisher (1958) is attributed as the first by Leimar and MaNamara (2023), while Van Cleve (2023) stated that Lewontin (1961) was the "first to introduce game theory to biology" (p1).

[2] Game theory has "transcended from its origins in mathematics into several disciplines in the past decades. Game theory today is used in the political and social sciences, in economics, and in psychology" (Traulsen and Glynatsi 2023 p1).

[3] ESS is a refinement of the "Nash equilibrium" (Nash 1950) in mathematics.

	Hawk	Dove
Hawk	**Fight** (to death, and populations dies out)	**Hawk wins** (and hierarchy develops of winners and losers)
Dove	**Hawk wins** (and hierarchy develops of winners and losers)	**Flee** (no resolution of conflicts)

Figure 2.1 - A pay-off matrix for Hawks and Doves meeting.

2023).

The evolution of animal "weapons" (eg: horns and antlers) in size can be seen as an example of the non-escalation of fights. The weapons are not there to cause damage, but to display the potential damage they could do and so to limit conflict. Male-male conflict often has stages of comparison before physical fighting. For example, red deer roar first as a signal of size and strength, then if one of the two contestants does not backdown, "parallel walking", where the two males can compare themselves side by side, and finally, "antler fights" (Leimar and McNamara 2023). But not all threat displays follow the predictions of game theory (Leimar and McNamara 2023).

A key insight of game theory is that dangerous contests (including fatal fighting) should evolve when the value of the win is so much greater than the value of the loss. "In an extreme case where there is no future reproduction for the loser of a contest, there is no incentive for a weaker individual to withdraw, and fatal fighting is the predicted outcome. An example is fighting between newly emerged honeybee queens. At most one of them can inherit the colony, and observations show that they fight to the death, even though they are likely to be relatives" (Leimar and McNamara 2023 p4). In such situations, weapons have evolved to damage or kill, not as signals. This is an example of a symmetrical contest.

Some contests are asymmetrical - ie: the cost/benefit for one player is much greater than for the other as in the "owner" of a territory and an "intruder". An ESS to settle the contest without fighting could be that an intruder withdraws if a resource already has an owner (figure 2.2). Observations of actual behaviour finds both evidence for and against game theory predictions (eg: speckled wood butterfly) (Leimar and McNamara 2023). Leimar and McNamara's (2023) conclusion was that "owners tend to win contests against intruders,

	Owner fights	Owner withdraws
Intruder fights	Fight (with inherent risks)	Owner loses territory and all invested in it
Intruder withdraws	Resolves conflict peacefully, and intruder seeks another area	Both lose

Figure 2.2 - A pay-off matrix for territory owner and intruder.

and the main explanation is likely to be that owners either have higher fighting ability or are more motivated, in the sense of estimating a higher value of winning" (p5).

Van Cleve (2023) presented two questions that challenge ESS: "(i) how do ESS models that focus on individual fitness capture the effects of kin selection or group selection? and (ii) how do ESS models account for recombination, mutation, migration and other evolutionary forces?" (p2). The first question relates to the "levels of selection" debate in evolutionary theory (ie: the level at which evolution "works" - eg: individual, group, gene), while the second question is the debate "regarding the relative role of natural selection vis-a-vis other evolutionary forces, such as mutation, recombination and migration, in explaining organismal phenotypes" (Van Cleve 2023 p2).

2.2. CO-OPERATION

Evolutionary game theory is also applied to co-operative situations [4]. For example, if an animal gives a predator warning call to the group, it benefits others, but increases their individual risk. However, "the call can also have the effect of making the predator fail to catch prey, therefore perhaps learning not to return to the local area, which is beneficial for the individual giving the call" (Leimar and McNamara 2023 p6).

An experimental example of co-operation with rats (Daniel 1942) created the situation where two individuals had to co-operate by taking turns in one sitting on a platform while the other fed without getting an electric shock. A pay-off matrix (as in figure 2.3) would predict co-operation. In such studies, "a common finding is that

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[4] Key articles are Trivers (1971), and Axelrod and Hamilton (1981) on the evolution of co-operation.

			Individual A
Individual B		Co-operate	Not co-operate
	Co-operate	**Both reward**	**A exploits B**
	Not co-operate	**B exploits A**	**Both no reward**

Figure 2.3 – A pay-off matrix for general co-operation.

rats to a large extent end up not co-operating" (Leimar and McNamara 2023 p6). However, these are artificial situations and the applicability to natural settings is not known (Leimar and McNamara 2023).

Game theory models tend to involve two individuals, which is simple to model but unlike everyday interactions with multiple individuals. However, modelling many individuals interacting is challenging (Leimar and McNamara 2023).

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3. PREDATOR-PREY RELATIONS

3.1. ANTI-PREDATOR DEFENCE

Anti-predator defences may be specific or general. The latter includes the use of body parts that evolved primarily for other purposes, like teeth. Specific defensive devices are body parts that evolved solely for anti-predator defence.

Sugiura and Tsujii (2022) reported the use of sharp genital spines (or "pseudo-stings") by the male mason wasp (Anterhynchium gibbifrons) against frog predators. "Male wasps were frequently observed to pierce the mouth or other parts of frogs with their genitalia while being attacked" (Sugiura and Tsujii 2022 pR1336).

Is this an example of a specific or general anti-predator defence? The spines perform "stinging" behaviour when attacked, but, unlike females, there is no venom. Hence, the term "pseudo-stings". The spines are not used to injure the female during mating. So, this would "suggest that the male genital spines function as an anti-predator defence" (Sugiura and Tsujii 2022 pR1337).

In an experiment that removed the spines in a sample of males, all seventeen wasps were eaten by predators compared to one-third of the healthy males (Sugiura and Tsujii 2022).

3.2. NOVEL PREDATORS

Anti-predator behaviours of prey co-evolve with strategies of predators to overcome these behaviours, except where predators are introduced into an ecosystem. These invaders can produce extinction of prey.

Banks and Dickman (2007) described three levels of "prey naivety towards introduced predators" (Tay et al 2023 p587):

- Level 1 - Not recognising the predator as a threat.
- Level 2 - Recognise a threat, but "respond inappropriately to the predator's hunting style" (Tay et al 2023 p588).
- Level 3 - The prey "recognise and act appropriately but are simply outperformed by the predator's superior hunting ability" (Tay et al 2023 p588).

Australia is a prime example of introduced predators (eg: feral cat; red fox) and the risk for terrestrial marsupials in the "critical weight range" (35 g - 5.5 kg) (Tay et al 2023). Tay et al (2023) compared eight species (and 178 individual animals) on their escape behaviour (using twenty measures). A 200 m runway was constructed with cameras to film the behaviour when a human chased the animal with a pole with a ball containing bells attached.

The twenty measures of escape were summarised into four dimensions: linear speed vs agility; acceleration style; reactivity; and gait characteristics.

The escape tactics were constrained by the animal's morphology. For example, bipedal macropods, like the banded hare-wallaby (Lagostrophus fasciatus), have fast acceleration in a straight direction, which is "suited to pursuit predators, and may also be appropriate against the ambush and pounce-pursuit strategies of cats and foxes if paired with high reactivity" (Tay et al 2023 p597). Quadrupedal bandicoots (eg: golden bandicoot; Isoodon auratus), on the other hand, have slower acceleration and speed, and are immobile. They usually retreat to vegetation cover, but are vulnerable to ambush/pounce-pursuit hunting of invasive predators. However, they "were more likely to use sudden changes of direction, which can be successful if pursued by a larger, less mobile predator or where there is sufficient vegetation cover to obstruct pursuit" (Tay et al 2023 p587).

A positive observation was that "animals increased the intensity of their response after repeated exposure, suggesting training could enhance effective anti-predator responses" (Tay et al 2023 p587).

This study only tested animals trapped by the researchers, who accepted that "the trapability of animals can create sampling bias where only bolder individuals within the population are caught... In addition, it is possible that individual differences would influence their responses to our experimental setup, and not all animals within our study were performing to their maximum physical capability. For consistency, the pursuit in all behaviour trials within this study was carried out by a single chaser, although we acknowledge that pursuit by a human is likely to be slower than being attacked by a real predator. Animals that were under-performing may not have been as intimidated by the chaser or were confused by the setup, and thus were not exerting themselves to escape down the runway" (Tay et al 2023 p597).

3.2.1. Invasive Species as Predator

Successful colonisation of a new area by introduced/invasive/non-native species depends on variables like abundant prey, low predation risk, low parasites and disease, high fertility and early reproductive maturity, as well as dispersion (Coticchio et al 2023).

Coticchio et al (2023) reported on the non-native Brown Widow spider (Latroductus geometricus) in Florida, USA. First recorded here in 1936, but subsequently reported as far afield as Kansas and California. This species is displacing the native Southern Black Widow (Latroductus mactans).

Data on both these species were collected in 2019 and 2020 in urban areas of Orlando, Florida. More Brown Widows were found and more viable egg sacs, suggesting greater fertility than Black Widows. When experimentally placed together, Brown Widow spiderlings "left their base web and aggressively stalked, captured, and preferentially consumed Southern Black Widows before cannibalising siblings. When approached by Brown Widows, Southern Black Widow spiderlings froze or fled, but did not initiate an attack. When cornered, they defensively counter-attacked" (Coticchio et al 2023 p178). The young of Brown Widows grew faster and matured earlier.

So, the invading Brown Widows are slowly replacing the native Black Widows due to greater female fertility, earlier maturity, and deliberate predation that is not through scarcity of prey. (Coticchio et al (2023) explained: Because we matched spiders by body size to within a half-millimetre and maintained them at the same temperature, light cycle, humidity, and on the same diet relative to their size, we can dismiss differences in body-size, hunger, or environmental conditions as triggers for predatory attacks by Brown Widows” (p181).

3.3. CAMOUFLAGE

Camouflage, which is defined as "the use of colour patterns and other morphological adaptations by an organism to reduce the probability of being detected or recognised by an observer" (de Alcantara Viana et al 2022 p1), is a key anti-predator strategy. Sixteen types of camouflage strategies have been classified (de Alcantara Viana et al 2022).

Camouflage strategies act upon different aspects of predator behaviour, including detection of a target (eg: background matching), recognition of prey (eg: masquerade), and attack (eg: eyespots).

Studies rarely compare the effectiveness of different types of camouflage. de Alcantara Viana et al (2022) performed a meta-analysis using the outcome measures of "search time" (ST) (ie: "the mean time to find and attack prey"; p2) and "attack rate" (AR) (ie: "the mean percentage of prey consumption"; p2). Sixty-three experimental studies of ST were found and 28 of AR.

Overall, predators took 63% longer ST on camouflaged than non-camouflaged prey, while camouflage reduced AR by 27%. Specifically, camouflage by masquerade, followed by background matching, and disruptive colouration were best for increasing ST, and the least effective were eyespots, and motion camouflage. Motion camouflage was most effective in reducing AR, however. Caterpillars benefited from camouflage most.

"Masquerade differs from the other strategies since while allowing detection, it works by reducing the probability of prey recognition by predators by increasing false signals, since the animal resembles an inanimate and uninteresting object from its surroundings, such as rocks, bark, twigs, leaves or even bird droppings" (de Alcantara Viana et al 2022 p2).

Experimental studies tend to concentrate on one camouflage strategy, but multiple strategies can occur simultaneously. "For example, many prey species can benefit from both disruptive colouration and background matching when selecting a tree trunk, where they can also mimic the substrate shape and texture, which also may favour masquerade. Additionally, many species can switch between different types of strategy along ontogeny, benefiting from the protection of each of them during a specific life-stage" (de Alcantara Viana et al 2022 p6).

3.3.1. Brightness Matching by Dragonflies

Iridescent colours have a variety of functions for animals, including to ward off competitors, to court females, and to avoid predators. In the latter case, this is the idea of brightness as camouflage in a bright visual background. This is "brightness matching" or a "counter-brightness" camouflage strategy (Cezario et al 2022).

An interesting example is the Morpho dragonfly (Zenithoptera lanei). A study of the iridescent wings of males suggested evidence of "camouflage against the water surface using a counter-brightness strategy. By 'brightness matching' the background visual properties of inland waters, males may hamper detection by conspecifics, prey, and visually oriented predatory birds, thus avoiding unwanted interactions" (Cezario et al 2022 p97). The UV-blue dorsal colours, and the closing and opening of the wings laterally that produces a flickering display "may function as an anti-predator strategy, flickering a camouflaged and confusing signal that birds have difficulties in targeting from certain distances" (Cezario et al 2022 p98). This did not apply against a savannah background.

Cezario et al (2022) argued that their work was "the first report of a terrestrial insect that exhibits brightness matching against the water surface" (p97).

"Brightness matching" or "counter-illumination" is known among marine animals, like the cuttlefish, which can match the brightness of the ocean bottom when observed from above, and match the brightness above, thereby disrupting their silhouette when observed from beneath (Cezario et al 2022).

3.4. ECOLOGY OF FEAR

The "ecology of fear" (Zanette and Clinchy 2019) describes the negative effects on prey, other than killing, of the presence of predators in the vicinity (eg: the cost of avoiding predators). "Overall, the negative effects on prey populations can be summarised as a reduction in foraging rates: scared animals eat less" (Galvez and Hernandez 2022 p467). For example, scatter-hoarder rodents that disperse (ie: cache) and consume seeds may reduce these behaviours in response to predators' scent. On the other hand, individuals willing to use sites with higher predator risks benefit by lower pilfering of their caches (Galvez and Hernandez 2022).

One example is the agouti-ocelot relationship, as studied in Panama by Galvez and Hernandez (2022). The Central American agouti (Dasyprocta punctata) (figure 3.1) scatter-hoard seeds during the fruiting period, and retrieve them in times of scarcity. The ocelot (Leopardus pardalis) (figure 3.2) is the predator, and they are detected mostly by odour in the dense forests.

(Source: Andra Waagmeester; public domain)

Figure 3.1 - Central American agouti.

(Source: US Fish and Wildlife Service; public domain)

Figure 3.2 - An ocelot (wearing a tracking collar in a wildlife refuge in Texas, USA).

Tagged seeds were placed in areas of low or high ocelot density in 2019, 2020, and 2021. Caches were also monitored for pilferage rates, and ocelot urine was used as a cue to predator presence.

Dispersal of seeds was less in areas with high ocelot cues, and there was significantly less cache pilfering in high density areas. The findings showed that "ocelots' cues generate a landscape of fear" (Galvez and Hernandez 2022 p471), which fits with previous research that prey eat less in the presence of predators.

One response to the fear of predators is to leave an area. Towner et al (2022) documented the example of white sharks (Carcharodon carcharias) responding to killer whales (Orconus orca) in South Africa. Gansbaai (off Western Cape Province) is a white shark aggregation site.

Data were collected in four ways:

i) Tourist boat surveys - Shark tour operators note the number of sharks present for their trade, and data covering 2008 to 2019 were available. Up to the killer whale predation in 2017, an average 5-8 white shark sightings per day, but this reduced to 1.17 after the predation, and remained as low in 2018 and 2019.

ii) Necropsies - External examinations of five shark carcasses in February to July 2017 showing killer whale attacks (four confirmed and one suspected). "Four of the five sharks had large tear wounds across the pectoral girdle and were missing their livers. Killer whale rake marks (scratch-like tooth impressions) were visible on two of the carcasses" (Towner er al 2022).

iii) Boat-based surveys of killer whales (between 2011 and 2019) - Of thirteen sightings of killer whales, mostly of a pair identified as "Port" and "Starboard", four in 2017 and four subsequently.

iv) 106 acoustically tagged white sharks between 2012 and 2019 - Before 2017, 3 to 8 individuals per day were detected in Gansbaai, and this dropped to 0-2 in 2017 and afterwards.

In summary: "A pair of easily identifiable killer whales were potentially responsible for predating on at least five white sharks in Gansbaai" (Towner et al 2022 p146). Declines in usual prey could be driving the killer whales' behaviour here (Towner et al 2022).

The researchers felt that the data showed a rapid response of emigration from Gansbaai by the white sharks when faced with the predation threat of killer whales. This allowed room for bronze whaler sharks (Carcharhinus brachyurus), whose numbers increased in the area. White sharks do predate on these sharks. Both sharks are attracted to this area because of the Cape fur seal colonies. Bronze whaler sharks are meso-predators here (ie: mid-ranking in the food chain hierarchy), and the absence of white sharks was a "competitive release" (Towner et al 2022). There will also be an impact on the prey (seals) of less white sharks.

Towner et al (2022) explained: "While killer whales are known to predate on white sharks in California..., to the best of our knowledge this is the first time that this has been documented in South Africa" (p146). For example, Jorgensen et al (2019) reported the flight of seventeen tagged white sharks in the Pacific in response to the presence of killer whales.

Emigration from an area has been observed on land with wild dogs in Tanzania when lion numbers increased, for example (Swanson et al 2014).

The researchers admitted: "Although we did not directly observe the killer whale pair predating on the white sharks, the rake marks and wounds on the carcasses were distinctly those of killer whales, and the same killer whale pair were observed in the area when predations were known to occur. The same killer whale pair were also implicated in predations on sevengill sharks... and bronze whalers in False Bay... [north-west of Gansbaai], indicating a level of experience and skill in hunting large sharks" (Towner et al 2022 p148).

3.4.1. Ecosystems

Rewilding projects that introduce large herbivores without their natural predators are likely to face overpopulation. Ecosystems have a "requirement for mortality" (Andre de Roos in Spinney 2022).

Cortez and Abrams (2016) began with this observation: "Intuition suggests that increases in the mortality rate of a species, due to predation, disease, harsh environments or other factors, will decrease its population size. This assumption underlies many conservation and management strategies. However, increased mortality of a species can have the counter-intuitive effect of increasing its population size" (p1135). Increased population size after increased mortality has been called a "hydra effect" (Abrams and

Matsuda 2005). The main reason is that increased mortality leads to less individuals competing for resources, and with this new abundance the survivors have more offspring.

The hydra effect is not inevitable and there are a number of variables involved (Cortez and Abrams 2016).

Non-lethal changes in the population can also have an impact on the population as a whole (eg: pollution; climate change). Such non-lethal factors may reduce foraging and this indirectly leads to mortality.

Studying the long-finned pilot whale (Globicephala melas) and anthropogenic disturbances (eg: ship traffic; sonar noise), Hin et al (2019) found that "short disturbances decreased survival among calves born to young females, while longer disturbances also reduced survival of calves born to older females and degraded female survival itself" (Hin et al 2021 p2).

Coming from a slightly different angle, Persson et al (2007) observed: "Predation on small individuals... leads to an overcompensating response because surviving prey mature more rapidly and achieve higher population reproductive outputs. Counter-intuitively, densities of small prey hence increase and not decrease when predators forage on such small prey individuals" (p1743). But "[A] drop in predator density causes prey to grow and reproduce more slowly and consequently produce lower abundances of vulnerable, small-sized prey" (Persson et al 2007 p1743).

Persson et al (2007) reported the application of these ideas to Lake Takvatn in Norway. The top predator, brown trout, was declining, and their prey (and competitors for invertebrates), Arctic charr, was increasing. During the 1980s "old stunted" charr were removed, "which caused an increase in the availability of small-sized prey and allowed the predator to recover" (Persson et al 2007 p1743).

3.4.2. No Predation

Invasive species that no longer have native predation risk could become more conspicuous in their social and sexual signals. Whiting et al (2022) studied in Jackson's chameleons (Trioceros jacksonii xantholopus) in "an unintended 'evolutionary experiment': accidental translocation of chameleons to a previously uninhabited, low-predation environment" (p1).

In 1972 around thirty chameleons escaped shipment from native Kenya on the Hawaiian island of Oahu. They have high population growth (9-12-month length of generation time and up to fifty young) and the potential for rapid evolution (50-65 generations). "On Oahu, there are few potential predators of chameleons (there are no snakes or lizard-eating raptors, and other potential bird predators are absent or rare...), while in Kenya, they are preyed upon by a wide range of bird, snake, and, occasionally, mammal predators" (Whiting et al 2022 p1).

Their normal colouring is dull green or brown to avoid predators with intense yellow-green colouring during courtship or to signal dominance.

An experiment tested the colouring of chameleons from Hawaii (no predators) and Kenya (native predators), including presenting bird or snake predators or a control (stick). Hawaiian chameleons had higher luminance contrast against the background generally than Kenyan chameleons. They also responded less to predators (ie: became less cryptic). This suggested evolution over approximately fifty years.

3.4.3. Humans as Super-Predators

Humans have been called a “super predator” (Darimont et al 2015) based on the number of animals killed. Zanette et al (2023) showed a fear of humans among animals visiting waterholes in South Africa's Greater Kruger National Park.

Playback was broadcast of humans talking (men and women in the local languages), lions (snarling and growling), hunting sounds (dogs barking and gunshots), and birds (non-predator controls), and the reactions of the animals were video-recorded. Over 4200 “exposures” (ie: broadcasts) were made at twenty-one waterholes over six weeks in the dry season (June-August).

The fear reaction to humans talking significantly exceeded all other sounds. Comparing humans talking to lions, “wildlife were twice as likely to run, and abandoned waterholes during the dry season in 40% faster time, upon hearing humans compared with hearing lions” (Zanette et al 2023 p2). The response to hunting sounds was weaker.

Nineteen species of animal were observed. “Considering each species separately, giraffes, leopards, hyenas, zebras, kudu, warthog, and impala all ran significantly more from humans upon hearing humans compared with lions, and rhinoceroses exhibited a similar tendency. Rhinoceroses abandoned the waterhole significantly faster upon hearing humans, as did elephants, hyenas, kudu, warthog, and impala, and zebras and waterbuck tended to as well” (Zanette et al 2023 p2).

In summary, 95% of species ran more on hearing humans talking than lions snarling and growling.

3.5. TOXINS

Toxins are "substances deployed by an animal to alter the physiology of a natural enemy" (Bucciarelli et al 2022 p64) [5]. They are usually divided into venoms, delivered by injection into the bloodstream [6], and poisons. "Poisons operate in a more passive manner, and must be ingested, inhaled, or absorbed through the skin to exert their effect. Poisons include a spectrum of substances, from a distasteful or noxious compound to potent neurotoxins" (Bucciarelli et al 2022 p64). Nelsen et al (2014) added a third type, known as "toxungens" (which covers toxins delivered via spraying, spitting or smearing - ie: no physical contact; eg: spitting cobra) (table 3.1).

TYPE	SPECIALIST DELIVERY SYSTEM OR MECHANISM	MECHANISM OF USE	EXAMPLE
Poison	No	Ingestion, inhalation or absorption through skin	Golden dart frog transferred with contact
Venom	Yes	Delivered into tissue via wound	Snakes with fangs
Toxungen	Yes	Delivered to body surface	Fire salamander spray up to 2 m

(Source: Nelsen et al 2014)

Table 3.1 - Three categories of toxins.

Venom has been defined and classified based on a number of criteria (Nelsen et al 2014):

a) Hierarchy and exclusiveness - eg: whether a venom

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[5] Toxins produced by living organisms are biological ones (or bio-toxins), as distinct from environmental toxins (that occur naturally like arsenic or mercury) and anthropogenic toxins ("man-made toxins") (Nelsen et al 2014).

[6] "Toxins delivered by passive contact or ingestion function best for defence, whereas those delivered via a penetrating wound are especially well suited for predation, and therefore are often under different selective pressures" (Nelsen et al 2014 p451).

is classed as a toxin or as a poison.

b) Source of secretion - eg: tissues, glands, cells.

c) Mode of transmission - eg: injection.

d) Purpose - eg: defence or predation.

e) Active application - eg: requires intentional application. But caterpillars of the genus Lonomia have stiff hairs that penetrate tissue and deliver venom, such that "[A] freshly deceased caterpillar could also do this every bit as effectively as a live specimen" (Nelsen et al 2014 p454).

Nelsen et al (2014) also made this distinction between organisms in terms of production and storage of toxins:

i) Autoaglandular - Organisms produce their own toxins, but lack a storage gland and a delivery system.

ii) Autoglandular - The toxin is produced by the organism and stored within a gland, but there is no delivery system.

iii) Heteroaglandular - The "poisonous organisms cannot produce their own toxic secretion, so they must acquire their toxins from other organisms. Lacking glands for storage, the toxins are often widely dispersed among the tissues. Exogenous toxins can be acquired in at least four ways: via ingestion (bioaccumulation), symbiotic bacteria, copulation, and maternal transfer to gametes and young" (Nelsen et al 2014 p458).

iv) Heteroglandular - Toxins acquired from other organisms, but stored within specialist glands.

The impact of toxins depend upon the dose. Because of the energetic cost of their production, users need to know the appropriate dose to achieve the desired end. For example, the tiger wandering spider was found to inject venom volume based on the size of the prey, and even not to use venom, but damage with the fang, the smallest prey (Malli et al 1998).

Toxin production can be endogenous or exogenous (Bucciarelli et al 2022). Venoms are produced endogenously by the animal via a cocktail of biochemicals. They are used in predation, defence, intra-specific competition (eg: male blenny fish), to parasitise hosts (eg: parasitoid wasps paralyse a host and lay the eggs within it), and to detoxify the own body from the venom of enemies (eg: tawny crazy ants and fire ants (Bucciarelli et al 2022).

Exogenous toxin production is where the diet of the individual gives them the toxin, or from prey (eg: non-poisonous snakes that store toxin from toad prey (Bucciarelli et al 2022).

Toxin production can vary with life stage, prey availability, interactions with other species, and intra-specific competition. For example, in the latter case, tadpoles of the common toad reared in greater densities had increased toxin production (Bokony et al 2016). While cone snails were found to have tow distinct types of venom - one for use against prey and one for defence (Bucciarelli et al 2022).

In the "evolutionary arms race" (or "antagonistic co-evolution") of predator-prey relations, some prey have evolved resistance to their toxic predators (eg: marine eels and the venom of sea snakes). "Further, the local abundance of the venomous sea snakes appears to be positively correlated with resistance, such that locations with a greater likelihood of sea snake predation have a greater level of resistance to the snakes' venom" (Bucciarelli et al 2022 p69). Other examples include rock squirrels and rattlesnake venom, grasshoppers and bark scorpions, honey badgers and cobras, and mongoose and snake venom (Bucciarelli et al 2022). Subsequently, predators should evolve a response (eg: different or stronger toxin).

The term, a "toxin-detoxifier interaction" (Kniskern and Rausher 2001) has been used to describe when "[P]rey produce toxins that impede or poison predators, and predators possess the trait(s) necessary to lessen or diminish the effects of the prey toxins" (Bucciarelli et al 2022 p75). For example, Pacific newts use the neurotoxin tetrodotoxin as defence against garter snakes, which have evolved resistance. The newts responded with ever-greater levels of tetrodotoxin (Bucciarelli et al 2022).

3.6. CAPTURING LARGE PREY

Spiders have evolved a wide range of predatory strategies including group hunting, specialised web traps, and aggressive mimicry. Ants are a dangerous prey for many spiders, but this does not stop their predation by some spiders (Aceves-Apericio et al 2022).

Aceves-Apericio et al (2022) presented an example of the Australian ant-slayer spider (Euryopis umbilicata) that captures much larger ants on vertical tree trunks. "The hunting sequence starts with a sit-and-wait period, followed by an acrobatic strike to the prey and successful capture by immobilising the prey. As they settle, the spiders attach a silk line (dragline) to the tree trunk surface. Then, they use a continuous line of adhesive viscid silk to strike and immobilize their prey..." (Aceves-Apericio et al 2022 p1).

The attack was acrobatic and very fast (less than one second). "The ant-slayer attaches its adhesive silk with a strike speed comparable to that of other non-web-building spiders such as wolf (0.05 m/s to 0.3 m/s) and jumping (1.5 m/s) spiders that rely on moving the entire body toward prey, although not as fast as the slingshot spider (4.2 m/s) that catapults itself and its web toward approaching prey" (Aceves-Apericio et al 2022 p3).

A sampling of prey found them to almost exclusively be the banded sugar ant (Camponotus consobrinus), which is twice the body length of the spider. Aceves-Apericio et al (2022) explained: "The evolution of specialised diets is uncommon among predators, and even less common when it involves large and dangerous prey. However, due to technological advances allowing for infra-red high-speed videography, we have been able to describe what appears to be an almost flawless strategy to capture dangerous prey. While relatively fast and easy access to unlimited prey is the likely main benefit, the potential costs of this strategy remain elusive" (p3).

3.7. PENGUINS AND NEST DEFENCE

“Increased human disturbance presents many challenges to wildlife. Animals regularly exposed to human disturbance (ie: living near human habitation or exposed to unregulated tourism) face new added pressures, such as habitat modification, introduced species and noise or light pollution” (Colombelli-Negrei and Katsis 2021 p195). Individual animals respond differently to such disturbances.

Colombelli-Negrei and Katsis (2021) investigated the difference in aggressiveness across four Little penguin (Eudyptula minor) colonies in South Australia in late 2020. The colonies varied in population size, and in level of human disturbance. The level of aggressiveness was measured in response to one of the researchers, who "approached the nest at a constant speed, crouched 0.5 m from the entrance of the nest, and extended a plastic pole (length 1.5 m) with a soft tennis ball at the end within 50 cm of the penguin's head for a period of 30 s" (Colombelli-Negrei and Katsis 2021 p197). Aggressiveness was scored from 0 to 4, based on behaviours like "attack" (defined as "neck fully extended, and physically attacked/pecked the soft ball at the end of the pole while hissing or growling"; Colombelli-Negrei and Katsis 2021 p198).

The nest defence (aggressiveness) of forty-three Little penguins was tested in this way. Each individual was tested twice on the same day. Just over half of the penguins attacked. Nest defence score was significantly associated with colony/island. The Little penguins were most aggressive on the island with the greatest amount of unregulated human disturbance (eg: unauthorised cars and bikes, dogs, and humans physically molesting the penguins).

This finding fits with the "personality-matching hypothesis", which states that "individuals with similar personality tend to aggregate together and select habitats that match their personality" (Colombelli-Negrei and Katsis 2021 p199). Applied to this study, the researchers explained: "Aggressive individuals may be more likely to persist in human-modified environments, perhaps because they can better protect themselves and their nests from potential predators (eg: red foxes or domestic dogs)" (Colombelli-Negrei and Katsis 2021 p200). But the "behavioural plasticity hypothesis" could also explain the findings - "little penguins in high-disturbance colonies may be actively adjusting their behaviour, becoming more aggressive over time as a result of experiencing increased threats" (Colombelli-Negrei and Katsis 2021 p200).

More aggressive parents have been found elsewhere to be poorer parents. So, on the islands with little human disturbance, there was no need for aggressiveness.

There were potential confounders to the study, like individual body size, and nesting density, which were not controlled for.

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4. FORAGING AND FOOD

4.1. UNUSUAL NUT STORAGE

Squirrels store nuts for later. Temperate-zone squirrels hoard the nuts in holes in trees or the ground, for instance, while sub-tropical squirrels can hang them on tree branches ("a behaviour thought to minimise germination or fungal infection in humid environments"; Xu et al 2022 p3).

Xu et al (2022) reported the case of two species of flying squirrel (Hainan flying squirrel (Hylopetes phayrei electilis) and Particolored flying squirrel (Hylopetes alboniger)) in Hainan Island, China, who "intentionally carved grooves encircling ellipsoid nuts or distributed on the bottom of oblate nuts and used these grooves to fix nuts tightly between small twigs" (Xu et al 2022 p2). These "surface preparations" of the nuts allowed them to be "'pressure fitted' between the two plant twigs in a way similar to the mortise-tenon structure in ancient Chinese architecture" (Xu et al 2022 p6).

The researchers observed 151 cached nuts suspended from over fifty tree and shrub species in three surveys separated by 44 and 61 days. Around half the nuts had disappeared between the first and third survey (and around one-fifth were new), but it was not possible to give a reason for the disappearances - use by squirrels, nuts fall to ground and germinate, or theft by other squirrels or other animals.

4.2. HUNGRY RISK-TAKING

Matty et al (2022) noted that animals pursue more risky behaviours when hungry as compared to well-fed. This was shown by these researchers in work with 1 mm-long nematode worms (Caenorhabditis elegans). These invertebrates showed less reaction to copper, which is toxic to them, when hungry. The conclusion was that "these animals employ riskier food search strategies when food-deprived" (Matty et al 2022 p1).

Reducing copper sensitivity allowed the animal to cross potentially toxic environments in the search for food. Insulin was found to be involved in signalling physiologically the change in behaviour.

After feeding, the reaction to copper returned to normal.

4.3. LOCUST CANNIBALISM

Cannibalism is "the killing and consumption of all or parts of a conspecific" (Chang et al 2023 p537), and it can supplement a diet with extra nutrition and energy. A number of animals show this behaviour, which can also occur to eliminate competitors or trigger mating. Egg cannibalism or eating of young can occur because of their relative size and/or defencelessness (Chang et al 2023).

There is strong selective pressure, however, for protective mechanisms against it. In the case of migratory locusts (Locusta migratoria), the defence is a pheromone (phenylacetonitrile; PAN) that repels conspecifics (Chang et al 2023).

Chang et al (2023) showed this in a series of experiments that included stopping the olfactory receptors for PAN, and genetically knocking-out PAN production. In the former case, these individuals were not repelled by locusts releasing PAN, and in the later, such locusts were attacked more than controls.

4.4. SELF-MEDICATION

"Plants are not only used as energy and nutrient resources for herbivores. Plants can be ingested because of their activity against host parasites and other pathogens" (Bautista-Sopelana et al 2022 p1). This is the "medicinal role of plants".

Bautista-Sopelana et al (2022) reported that male great bustards (Otis tarda) preferred certain plants with bioactivity against parasites and other pathogens (the common poppy and the purple viper's bugloss) during the mating season. "Males' immune system is weakened during the mating season because of their investment in secondary sexual characters and sexual display" (Bautista-Sopelana et al 2022 p1). This is evidence of self-medication by the birds.

Great bustards are mostly vegetarians, but males also consume blister beetles during the mating season (Bravo et al 2014). "Blister beetles contain cantharidin, a highly toxic monoterpene that could have positive effects in controlling the parasite load of the host" (Bautista-Sopelana et al 2022 p2).

Heneberg (2016) argued that consumption of these beetles was the males seeking sexual arousal not the anti-pathogen effects. Bautista-Sopelana et al (2022) accepted: "Both effects are not mutually exclusive" (p10). However, the explanation of sexual arousal does not hold for the two plants studied (Bautista-Sopelana et al 2022).

de Roode et al (2013) proposed five conditions for a food to be seen as a medication as in self-medication (Bravo et al 2014):

i) Ingestion or external application of the substance/chemical through a food.

ii) The ingested chemical should enhance the fitness of the consumer.

iii) There is some cost to the ingestion (eg: chemical partly toxic or not well tolerated in large doses).

iv) The behaviour should be observed in the natural environment, not in artificial situations (eg: zoo; laboratory).

v) There must be a threat or risk of future threat (eg: parasite infection).

4.5. OPTIMAL DIVING

Air-breathing animals that hunt for food underwater are limited by their ability to store oxygen. Optimal diving models suggest that the animals should stay underwater until the oxygen store is depleted (ie: the maximum duration for an aerobic dive or aerobic dive limit (ADL)). The ADL is calculated by "dividing an estimate of oxygen stores by an estimate of the rate at which oxygen is used during a dive" (Houston 2021 p189).

Houston (2021) argued that optimal diving "takes both food and oxygen into account, and so in general both factors influence dive duration and the optimal fraction of maximum oxygen stores" (p191). In other words, divers do not need to stay underwater for the maximum amount of time. This was supported by data from whale species.

4.6. FOOD RESOURCE MANAGEMENT

Searching for food (exploration) requires energy, and if food availability is variable, then energy use will vary also. Learning and memory are shortcuts to save energy between exploration and exploitation of food source. This is information updating behaviour, or information or knowledge maintenance, and sampling is an important aspect of it. "In a foraging context, sampling is often observed when an individual is presented with multiple food sources: first, the animal explores the available sources, then repeatedly visits each source to determine quality and consistency... If an individual stops visiting multiple sources and only forages from one, it has moved from the information updating phase to the pure exploitation phase" (Benedict et al 2021 p154).

How often to sample the environment? The simple answer is when the information gathered is greater than the cost of sampling. "Oversampling could be costly in terms of physical effort and lost opportunities for other activities while undersampling could lead to missing critical environmental changes or making poor choices about which resources to prioritise" (Benedict et al 2021 p154). Also the predictability/unpredictability, and harshness/abundance of the environment will influence this behaviour. "Animals would be expected to update information more when conditions are both unpredictable and harsh, as it is more critical to know where food is available in case one food source fails" (Benedict et al 2021 p154).

Benedict et al (2021) investigated this prediction in the mountain chickadee (Poecile gambeli), a wild food-caching bird. Data from 2014-2020 in the Sierra Nevada, California were available on nearly 500 individuals. Environment harshness was calculated using average temperature and snow depth. Throughout the study area, feeders containing seeds were distributed, and sampling was defined as a visit to determine if food was present. Chickadees selected one seed per visit, and left to eat or cache elsewhere.

The chickadees visited more feeders when the environment was harsher and more unpredictable. Benedict et al (2021) explained: "Chickadees had a preferred feeder that they foraged from more than the others, and yet they continued to use other feeders. Our results support the hypothesis that when birds experienced a harsher and less predictable environment, they invested more in maintenance of previously learned information by updating such information more frequently. Having the most updated information may be beneficial in case previously available food sources become unavailable, so birds would be able to quickly find an alternative source" (p162).

Individual passive integrated transponder (PIT) tagging of the birds allowed the researchers to see that "individuals with better spatial learning and memory abilities engaged less in information updating, as indicated by smaller feeder use breadth, than birds with worse abilities even when accounting for annual variation and age effects" (Benedict et al 2021 pp163-164). Cognitive abilities were tested by varying the feeders that would dispense seeds (ie: the use of radio-frequency identification (RFID)-enabled "smart" feeders that responded to the PIT tags). Age-related experience was also found to influence sampling behaviour.

4.7. SOCIAL FORAGING

Social foraging occurs when individuals come together (even co-operate) around "resource hotspots" (particularly when the prey are transitory or ephemeral). An example of a resource hotspot in the ocean is krill aggregations. Cade et al (2021) collected data by different methods on social foraging by south-east Atlantic humpback whales (Megaptera novaeangliae), and north-eastern Pacific blue whales (Balaenoptera musculus). Data were collected using biologging tags, acoustic prey mapping, passive acoustic recording of calls, and remote sensing of surface currents on South Africa's west coast, and Monterey Bay, off the US west coast.

Rorqual whales can use three strategies for foraging (Cade et al 2021):

i) Individual - eg: school of anchovy consumed in a single gulp.

ii) Collective - (a) depletable or (b) ephemeral prey. The former includes schools of fish "herded" by different species and/or groups of whales blowing bubbles (so-called "bubble nets"). In the latter case, ephemeral refers an aggregation that is "so large that it is not meaningfully depleted by foraging whales" (Cade et al

2022 p252). "Supergroups" of predators (eg: 30-180 whales) might be involved here.

Cade et al (2021) found that whales made calls to recruit other whales in the presence of ephemeral prey hotspots (ie: large but temporary). The advantages of creating a supergroup for the individual outweighed the usual disadvantages of having competitors for a food source. This is evidence of a social foraging strategy.

Telling others about the food source (ie: information-sharing) and encouraging them to come and join in was a means to "avoid the pitfalls associated with finding patches individually" (Cade et al 2021 p261).

Cade et al (2021) proposed a number of reasons for the formation of such supergroups of rorqual whales. These included that the prey were so abundant that large numbers of predators do not deplete the number. The researchers estimated that one prey patch observed on 16th August 2017 would take forty blue whales nine hours to consume. Another reason is that environmental conditions mean that the krill hotspots, for instance, are transitory (eg: on a scale of hours).

4.8. REFERENCES

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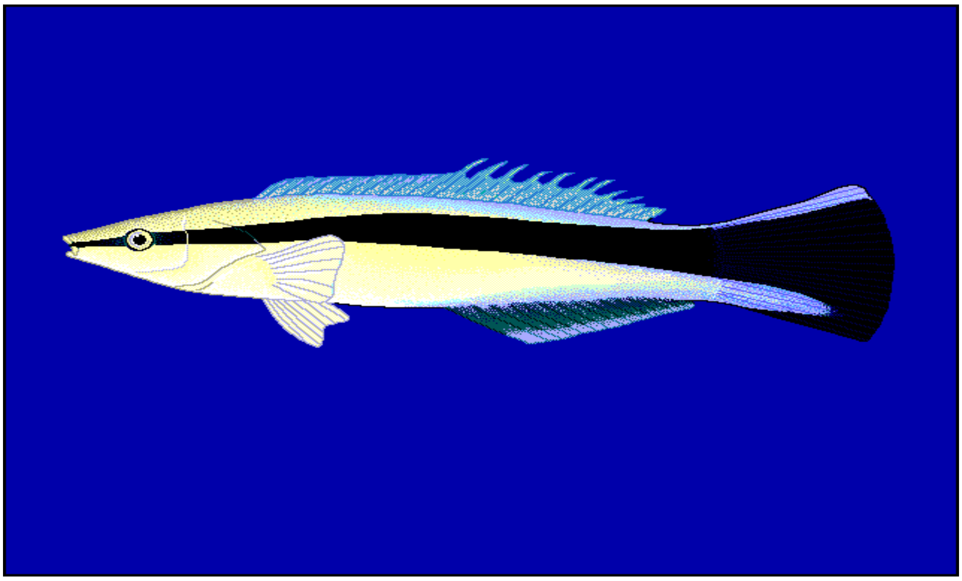
5. ANIMAL COGNITION

5.1. CLEANER FISH AND THEORY OF MIND

The ability to represent another's point of view is known as "Theory of Mind" (ToM). It has been studied in non-human primates, like chimpanzees, extensively, and in a few other animals. An example of an experiment with chimpanzees involves a subordinate and a dominant individual and food. Normally, the former would not take the food, but if the food is placed out of view of the dominant individual and within the view of the subordinate individual, the subordinate is more likely to take the food (Hare et al 2000). ToM is shown here in that the subordinate individual is able to take the dominant individual's perspective and know what they can or cannot see.

In terms of non-primates, McAuliffe et al (2021) reported a study on ToM and the bluestreak cleaner wrasse (Labroides dimidiatus) (figure 5.1) based on the methodology used with chimpanzees. This cleaner fish feeds on ectoparasites and dead skin cells of other (client) fish, who accept this "service", but also on client mucus (which causes the client to become aggressive). A client fish is approached by a female and male cleaner, say. The female could "cheat" by consuming mucus, and the client fish would leave (if not attack). The solution is "the larger males punish a cheating female partner with aggressive behaviour such as chasing and biting, causing her to behave on average very co-operatively during joint inspection" (McAuliffe et al 2021 p2). But if she has ToM ability, she can eat mucus when the male partner cannot see her. McAuliffe et al (2021) tested this possibility in two experiments.

In Experiment 1, a female cleaner was offered two food items - equivalent to dead skin cells or mucus. In half the trials, a male was watching in a separate



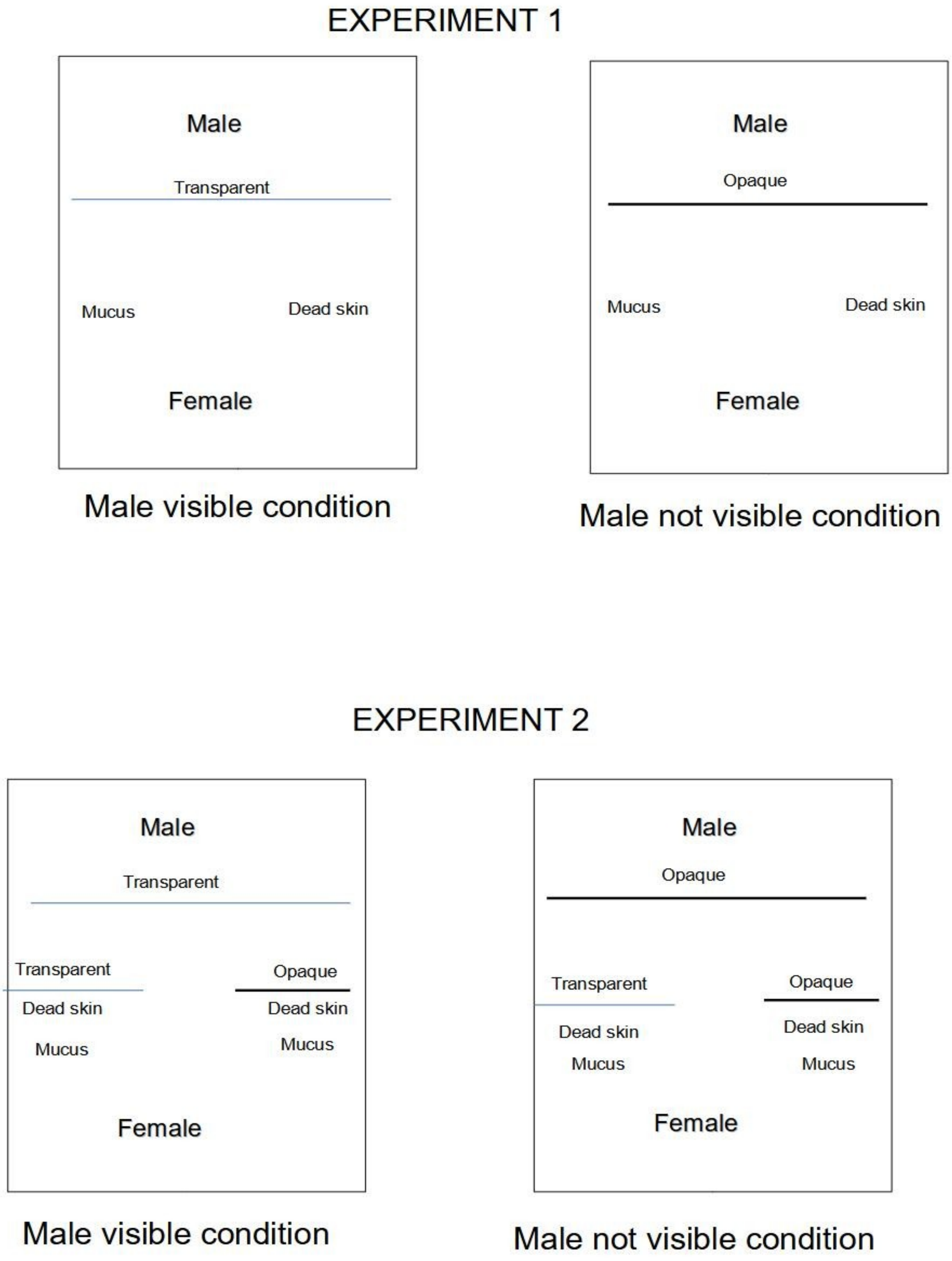
(Source: Robbie N Cada at Fishbase; public domain)

Figure 5.1 - Drawing of bluestreak cleaner wrasse.

compartment of the tank ("male visible condition"), who was released into the female compartment after the choice, and in the other half there was no male watching ("male not visible condition"). Technically, the make was hidden behind an opaque screen. Females were more likely to "cheat" (ie: choose the "mucus") in the "male not visible condition".

In Experiment 2, females were given a choice to feed where a male could or could not see them (with a male watching or not). Females were more likely to feed out of view of the male in the "male visible condition" (figure 5.2).

The females' behaviour in both experiments suggested evidence of ToM (ie: the ability to know what the male could or could not see).



(After figure 1 McAuliffe et al 2021)

Figure 5.2 - Representation of two experiments by McAuliffe et al (2021).

5.2. GIRAFFES AND STATISTICS

"Statistical inference" or "reasoning about probabilities" appears in pre-school children, and some see it as unique to humans. In relation to non-humans, a few experiments have been tried with great apes, macaques, and parrots, for instance (Caicoya et al 2023).

Caicoya et al (2023) experimentally tested giraffes (Giraffa camelopardalis) (two males and two females in a zoo in Spain). Each animal was presented with two containers of food out of reach but visible - a highly preferred food (carrots) and a less preferred one (zucchini). The giraffe was trained to signal which food they wanted when a keeper picked one food from each container in different hands. The experiment involved three conditions with variations in the two containers:

1. (a) 20 carrot/100 zucchini pieces vs (b) 100 carrot/20 zucchini pieces. Statistical inference is involved in that one piece picked from (b) is more likely to carrot than from (a).

2. (a) vs (c) 20 carrot/4 zucchini pieces. Caicoya et al (2023) stated: "In this condition, we predicted that giraffes would preferentially select the second container if comparing relative frequencies, but show no preference if comparing absolute quantities of the preferred foods" (p5).

3. (d) 57 carrot/63 zucchini pieces vs (e) 3 carrot/63 zucchini pieces.

Each giraffe performed twenty trials, and with the exception of five trials, all the expected containers were chosen - 1b, 2c, and 3d. It appeared that the relative frequency was being used to influence food choice.

The second set of tasks included the variable of physical barrier. A container included an accessible and inaccessible area. In one container the same number of food pieces (20 carrot/20 zucchini pieces) were in both areas, but in the other container, it was 20 carrot/4 zucchini (accessible) and 20 carrot/36 zucchini (inaccessible). It was predicted that "if giraffes could also use their understanding of physical barriers when making statistical inferences, they should have preferentially selected the second container" (Caicoya et al 2023 p5).

Three of the four giraffes failed this task. "Given that this task requires the ability to integrate information across multiple cognitive domains, the lower performance of giraffes in this task might suggest that, whereas they can reliably make inferences based on the relative frequencies of objects, their ability to integrate information across cognitive domains may be more limited" (Caicoya et al 2023 p4).

Overall, four giraffes showed that they could "reliably make statistical inferences based on the relative frequencies of two different food types" (Caicoya et al 2023 p3). Caicoya et al (2023) ended: "In evolutionary terms, statistical abilities might provide crucial fitness benefits to individuals when making inferences in a situation of uncertainty, and it should, therefore, not be surprising if these abilities are widespread across animal taxa" (p4).

5.3. MEMORY FOR PREY LOCATION

Food caching animals "possess extraordinary spatial memory that is adaptive in the context of locating stored food... [But] memory formation and retention is energetically expensive, and thus, the information stored in memory is curated adaptively... Selection thus favours the formation of memories that lead to adaptive behaviour when the memory is later recalled" (Sergi et al 2022 p707).

Web spiders are interesting to study here. "Some remember the overall layout of their web and their position in it... Some remember the location in the web where they captured prey, and alter their webs to make them better able to capture prey in the web location where past prey captures have occurred... Many web-building spiders also remember the contents of their web, such as the presence of prey, the relative size of captured prey, and even the relative number of captured prey" (Sergi et al 2022 p708).

Sergi et al (2022) studied the Western black widow spider (Latrodectus hesperus) which builds a three-dimensional cobweb that captures both terrestrial and flying prey. Adults females captured in Oregon were used in the experiments. An individual spider was placed in an experimental enclosure and allowed one week to construct a web, before being randomly assigned to the control or experimental condition. In each case the spider was given a cricket which was placed on the web. In the experimental condition the researchers stole the cricket, while the cricket was immediately put back in the control condition. Sergi et al (2022) described the procedure thus: "In each treatment in which we stole the cricket, we allowed spiders to wrap crickets in silk, detach it from the web sheet, and begin to carry it back toward their retreat suspended from a silk line attached to the spinnerettes. We then used a forceps to steal crickets from spiders" (p710).

If the spider has a memory of the prey, it will search for the missing cricket. Video recordings showed that 97% (38 of 39) spiders in the experimental condition searched for the prey (for an average of ten minutes), while only 27% (8 of 30) in the control condition (for an average of 3.5 minutes).

The findings suggested that "black widows do form memories of captured prey and are much more likely to search about their web after experiencing the theft of a prey item" (Sergi et al 2022 p711). Search duration was longer for larger prey.

5.4. SLEIGHT OF HAND

Garcia-Pelegrin et al (2023) tested three New World monkey species - yellow-breasted capuchin monkey (Sapajus xanthostemos), Humboldt's squirrel monkey (Salmiri cassiquiarensis), and common marmosets (Callithrix jacchus) - with "sleight of hand" tricks. This type of magic "capitalises on the observer's expectations of specific manual movements, making it an optimal model to investigate the intersection between the ability to manually produce an action and the ability to predict the actions of others" (Garcia-Pelegrin et al 2023 p1803).

The "French drop" was used where "a food reward was first shown to the subject with one hand and then either transferred to the opposite hand (if a real transfer) or retained in the same hand (if a sleight of hand magic trick). Following this, the subject was allowed to choose which hand contained the reward, and the hand was opened upon selection. If chosen correctly, the subject was allowed to consume the reward within" (Garcia-Pelegrin et al 2023 p1805). The trick involves the thumb holding the object ("precision grip" version), while an alternative version was developed that did not depend on the thumb ("power grip" version). It was predicted that the species that could perform the trick in theory in the precision grip version (capuchins and squirrel monkeys) would be fooled, but not the species that do not have the thumb control (marmosets). All species could perform the power grip, and so will be fooled by the trick.

"When observing the French drop, only the species with full or partial opposable thumbs were misled by it, just like humans. Conversely, the adapted version of the trick misled all three monkey species, regardless of their manual anatomy. The results provide evidence of a strong interaction between the physical ability to approximate a manual movement and the predictions primates make when observing the actions of others, highlighting the importance of physical factors in shaping the perception of actions" (Garcia-Pelegrin et al 2023 p1803). For instance, only 6% of the marmosets choose the incorrect answer in the precision grip version but 93% in the power grip version of the French drop.

This fits with the concept of "mirror neurons" - ie: watching another's actions activates these neurons in the brain as if performing the action. This is advocated by the "common-coding theory" (Prinz 1997). So, "[W]hen we produce actions, our common-codes instruct our movement, whereas when we perceive actions, our common-codes allow us to detect the goal of the action being perceived. Consequently, perceiving and performing a particular action should activate the same common-codes, and the more similar an observed action is to the way the observer would perform it, the stronger the activation of these common-codes" (Garcia-Pelegrin et al 2023 p1803). For example, expert human capoeira dancers have a stronger activation of mirror neurons when watching other capoeira dancers than ballet dancers (Calvo-Merino et al 2005).

5.5. VIRTUAL ENVIRONMENTS

Studying the navigational behaviour of animals in physically controlled experimental environments is restricted compared to the wild. Virtual environments, however, could overcome this problem.

For example, Washburn and Astur (2003) trained four macaques to navigate a simple 3D maze to find an object. These animals were successful, but it took over 3500 trials of training and testing (Allritz et al 2022).

Dolins et al (2017) trained four chimpanzees with a virtual "T-maze" with two or three choices of direction. "All chimpanzees succeeded on the T-mazes with two choice points, and two chimpanzees succeeded eventually on T-mazes with three choice points" (Allritz et al 2022 p2). It took between 100-400 trials to learn (and the ability was similar to 3-6 year-old human children) (Allritz et al 2022).

Allritz et al (2022) trained six zoo-based chimpanzees on a touch-screen virtual environment that represented a naturalistic foraging situation. The test involved collecting four or five pieces of virtual fruit. In early trials, the fruit was initially visible on the screen, but latter it was hidden and required movement to find it (eg: the use of landmarks as clues to the direction). "The chimpanzees exhibited signature behaviours reminiscent of real-life navigation: They learned to approach a landmark associated with the presence of fruit, improving efficiency over time; they located this landmark from novel starting locations and approached a different landmark when necessary" (Allritz et al 2022 p1).

5.6. CHILDREN VS CHIMPANZEES

"Attentional set shifting" is "the ability to quickly switch attention between different rules, instructions or 'mental sets', allowing individuals to adjust to changing environments. An attentional set results from a bias to direct one's attention preferentially to one stimulus or group of stimuli over others, leading to heightened processing, with inhibited processing of other stimuli. This processing bias typically results from the individual’s learning history" (Reindl et al 2023 p1). It has been studied in human children and in non-humans with different methods, including the use of language with humans.

Reindl et al (2023) developed the "shifting shelf task" which could be used with all. The researchers described the procedure thus: "participants are presented with two sets of shelves, each containing an upper and a lower shelf and holding a set of maximally four cups (two cups per shelf). In training, with changing left-right position of cups, participants learn which cup is consistently rewarded on each set of shelves. The rewarded cups differ between the sets, eg: on the right set, the green cup on the bottom shelf is correct, on the left set, the pink cup on the top shelf is rewarded. In the test, both sets hold the same four cups (eg: yellow, pink, green and orange). To choose the correct cup on each set participants need to shift their attention towards the correct cup based on the location (left-right) of the set they can currently choose from. If participants fail to switch attention, they will commit a specific type of mistake — a switching mistake, defined as choosing the cup that is rewarded on the other shelf — instead of choosing a cup that is never rewarded ('random' error). Switching mistakes are a signature of failed attention shifting (or perseveration)" (Reindl et al 2023 p3).

In their first experiment, forty-six 3-5 year-olds in Scotland were tested. No verbal instructions were given, and during the training had to learn by trial and error. In the testing phase, each child performed 36 trials. The success rate was significantly above chance. Subsequently, another 178 children were tested.

Next, fifty-three chimpanzees at two sanctuaries in Africa (in Kenya and Uganda) were tested.

Overall, five year-old children made significantly less errors than chimpanzees (80% vs 52% correct switches), and three and four year-olds (50% and 59% correct respectively).

Reindl et al (2023) explained: "We found evidence for performance improvement over the pre-school years: older children made fewer mistakes than younger children and were less likely to make a mistake directly after a switch (ie: when the need for attentional set shifting is greatest). If mistakes were made, older children were more likely to make switching mistakes (indicating a failure to switch attention), whereas younger children were more prone to choosing a cup that has never been rewarded" (p7).

As with previous research (eg: Herrmann and Tomasello 2015), it was found that "attention shifting in 5-year olds was significantly better than in chimpanzees in a task in which participants had to monitor and switch attention between two apparatuses, whereas 4-year olds and chimpanzees performed on a comparable level" (Reindl et al 2023 p8).

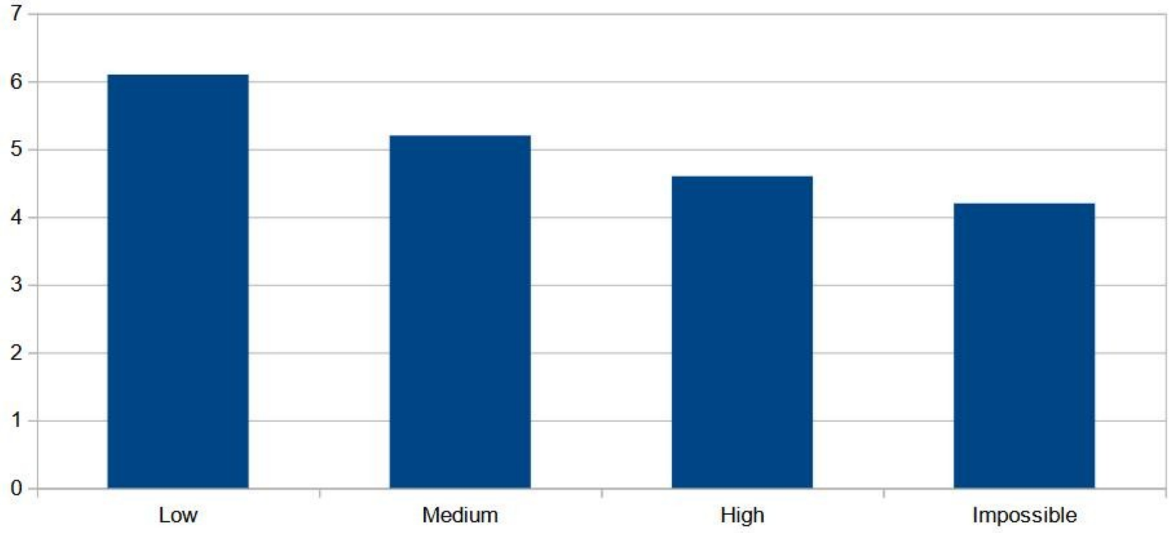
Attentional set shifting is part of "executive functions", which describe the range of cognitive processes involved in higher cognitive functions, and complex goal-directed behaviour (Reindl et al 2023). The findings of Reindl et al's (2023) experiments suggested that "chimpanzees and young children share attentional set shifting capacities, but that there are unique changes in the human lineage from 5 years of age" (Reindl et al 2023 p1).

5.7. SPEED-ACCURACY TRADE-OFF

The "speed-accuracy trade-off" is "the tendency for animals to trade decision speed against decision accuracy during problem solving" (Ng et al 2021 p59). For example, in relation to task difficult, bumble bees spend less time on easy colour discrimination tasks, and more time on more difficult versions of the task (Dyer and Chittka 2004)). The ability to invest different time intervals on tasks suggests a "time sense" or "interval timing capacity" (Ng et al 2021).

Ng et al (2021) designed an experiment to test time allocation to low, medium, high, and impossible difficulty colour discrimination tasks by European honey bees (Apis mellifera). Bees were taught to associate one colour with a reward, and then presented with a forced choice. The low difficulty task, for example, might be blue and green, where blue is associated with a reward, while the impossible task might be two almost identical shades of blue. Thirteen bees were trained and tested. The time to make a decision (ie: land on the colour) was recorded.

There was a significant difference in decision time between the tasks based on difficulty of task (figure 5.3). The decision time was quicker with the impossible task. There was no difference in accuracy between the tasks (ie: correct choice for reward). This suggested that the bees had a time allocation strategy.



(Source: Ng et al 2021 figure 3 p62)

Figure 5.3 - Average decision time based on task difficulty (seconds).

Ng et al (2021) explained that "in the impossible task, the amount of time allocated to the task would never improve accuracy as the task was unsolvable, and all choices have the same probability of being correct. In this case, bees opted to switch to a strategy that emphasised speed and fast guessing (ie: where speed reaches a ceiling and random choices are made) over accuracy; likely optimising resource collection even if bees chose the distractor in approximately 50% of choices. While this low accuracy would reduce foraging efficiency, nectar collection rates are also a function of speed, and therefore reducing time investment can be an efficient strategy to achieve optimal foraging even when under difficult foraging conditions” (p62).

Note that the findings are the opposite to those with bumble bees. Ng et al (2021) offered this possible explanation: “Bumblebees evolved in temperate conditions with small and widely distributed flower resources... In contrast, honeybees evolved in tropical environments where large trees in flower suit the dance language communication system to recruit nestmates... This dance language may result in a greater emphasis on speed in honey bee workers as they can rely on quickly exploiting social information, while bumble bees are more reliant on individual trial and error information that may require an emphasis on accuracy... However, speed-accuracy trade-offs during an impossible task have not been tested in bumble bees and it is unclear whether they will also switch to a fast guessing strategy when the task is sufficiently difficult” (p63).

5.8. TOOL SET USE

"Tool use" has been reported in a number of species. It involves the use of one object in another way to achieve a goal (eg: using a twig to reach an object beyond arm's length). "Associative tool use" (or "tool sets") is the use of "more than one tool to achieve a single goal" (Osuna-Mascaro et al 2023 p849). It is the next level of cognitive complexity for a variety reasons, "such as different tools having complementary functions, each tool requiring different movement patterns, a higher total number of spatial relationships to consider, or even a need for sophisticated action planning" (Osuna-Mascaro et al 2023 p849). This ability, Osuna-Mascaro et al (2023) stated, has been reported in the wild only by chimpanzees (eg: Nishihara et al 1995), and Goffin's cockatoos (O'Hara et al 2021).

A chimpanzee example is "termite fishing" - ie: getting termites from their subterranean nest - requiring "a perforating stick (short and rigid) used to pound a hole in the termite mound, and a fishing probe (long and flexible), to access the deeps of the mound and extract aggressive soldier termites" (Osuna-Mascaro et al 2023 p849).

Osuna-Mascaro et al (2023) tested ten Goffin's cockatoos (Cacatua goffiniana) (housed at a lab in Austria) in three experiments. Each experiment required the use of a previously unknown tool set (a short, and a long stick) to get a food reward from a "puzzle box". in the first experiment, the small stick was needed to tear a wrapping membrane, and the long stick to reach the reward. This experiment was performed multiple times and gradual improvement (learning) was shown. Five cockatoos eventually succeeded. They "innovated the puncturing and tearing of a membrane, a yet unreported mode of avian tool use" (Osuna-Mascaro et al 2023 p853).

These five cockatoos performed the second experiment where access to the reward required either the tool set or a single tool (and this was varied by the researchers). This experiment tested cognitive flexibility. "The five individuals who proceeded into this experiment chose the correct tool above chance expectations from the start. Nevertheless, they still improved as the experiment progressed" (Osuna-Mascaro et al 2023 p854).

The third experiment added an extra element that required movement (eg: a staircase to climb in the middle of problem solving). This experiment tested whether the birds would take the tools with them in the stages of solving the problem. Three individuals transported the tool set significantly above chance.

Osuna-Mascaro et al (2023) concluded from their findings that "tool set use by Goffin's cockatoos results from individual innovation but seems to be within the capacity of the species (notably, in a more limited capacity, also in wild settings). The identification of a tool set in anticipation of future need additionally requires the cognitive capacity to make task-dependent decisions about when to transport more than one tool. This ability seems to be constrained by general cognitive flexibility and a possible trade-off between attention and task effort. It thus remains limited to certain individuals" (p855).

5.9. RECOGNITION OF OWNER'S VOICE

Background - "Infant-directed speech" (Kaplan et al

1995) involves shorter utterances, more repetitions, and elevated pitch, for instance. It has also been called "caregiver speech" (Rowland et al 2003) to cover its adaptation to pets in "pet-directed speech" generally, or specifically "dog-directed speech" and "cat-directed speech" (CDS). Experiments with dogs (eg: Ben-Aderet et al 2017) found that they respond to dog-directed speech more than normal speech ("adult-directed speech"; ADS).

Aim of Study - To investigate the response of cats to CDS and ADS.

Participants - Sixteen indoor cats (Felis catus) whose caregivers were veterinary students in France and who volunteered to participate.

Design - Field experiment (ie: conducted in the caregiver's home).

Procedure - Recordings of the caregivers and strangers using CDS and ADS were played to the cats, as well as a female stranger and the caregiver calling out the cat's name. The response of the cat was video recorded and scored for ten seconds after the playback.

Findings - i) The cats responded to their caregiver calling the name more than the stranger, which suggested discrimination of the two voices (and recognition of their caregiver's voice).

ii) The cats responded to CDS by their caregiver over ADS, but not so with a stranger.

Conclusion - The cats responded to their caregiver's voice, and particularly to their use of CDS.

Limitations of the Study - i) Small sample size.

ii) Caregivers were veterinary students with limited demographic variability, and so the findings might not be generalisable.

Strengths of the Study - i) The experiment took place in the cat's home to control for potential stress of a new environment.

ii) Recordings of speech from direct human-cat interactions.

Comment - "Although cats have a reputation for ignoring their owners, a growing body of research indicates that cats pay close attention to humans... Cats can very much learn that specific vocalisations have certain meanings” (cat behaviour scientist, Krisyn Vitale in Lewis 2023).

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6. EVOLUTION OF NEST-BUILDING AND NESTS

6.1. OVERVIEW

Mainwaring et al (2023a) began with this observation: "Nests are built by a range of vertebrate and invertebrate taxa — including fishes, reptiles, amphibians, birds, mammals and insects — to house vulnerable eggs and offspring. Nest structures typically hold the eggs of oviparous species and the offspring of both oviparous and viviparous species and, therefore, play a key role in achieving reproductive success" (p1).

The view of naturalists in the mid-19th century (eg: Alfred Russel Wallace) was that nest building by birds is not instinctive, but today the opposite view holds. Experiments that control the early environment (eg: Collias and Collias 1962) (ie: hand-rear) find that birds build nests similar to others of their species without having seen other nests. Though experience does play some role in aspects of nest building (Healy et al 2023).

In understanding the evolution of nest-building and nests, Mainwaring et al (2023a) identified four conceptual themes in the research:

i) The function of nests - The evolution of nests occurs under selection pressure from predators (ie: to stop them accessing the inhabitants), and from sexual selection (ie: nests "serve as extended phenotypic signals of the builder's quality"; Mainwaring et al 2023a p2). So, "while natural selection favours small and inconspicuous nests, sexual selection favours larger and conspicuous nests..." (Mainwaring et al 2023a p2).

Nest building in mammals, for example, occurs for reasons other than maternal, and beyond the function for birds (eg: resting; hibernation) (Deeming 2023).

ii) The evolution of nest characteristics.

iii) Large communal nests in harsh environments - eg: eusocial insects like termites in arid regions of Africa and Australia.

iv) Nests today - "Nest-building animals face a range of issues in the Anthropocene, including the effects of increasing temperatures that result in sea-level rises that inundate nests, skewed offspring sex ratios in species with temperature-dependent sex determination, and the negative effects of including anthropogenic materials into their nests. It is well established that seabirds and terrestrial passerines incorporate a range of anthropogenic materials, such as plastic fishing nets, cigarette butts and food wrapping into their nests, and that such anthropogenic material sometimes causes birds harm" (Mainwaring et al 2023a p4).

6.2. FUNCTION OF NESTS

Nest-building is under pressure from both natural and sexual selection. In the former case, the best nests to provide for the offspring. "Sexual selection on nest-building behaviour can arise if the nest protects against sperm competition from sneaker males, or if one sex prefers to spawn in nests built in a certain way, and builders of attractive nests therefore gain increased access to opposite-sex gametes. Furthermore, when nest-sites are limiting and primarily (or only) site-owners gain access to gametes, then intra-sexual competition for nest-sites is also sexually selected" (Svensson and Kvarnemo 2023 p1) [7].

Svensson and Kvarnemo (2023) used the example of ray-finned fishes, where the males are often the nest builders. Firstly, the location of the nest is important. Practically, this includes hiding from potential predators (eg: more vegetated sites), and females can choose the male based on the nest location.

A holder of a large nest site will benefit as more eggs can fit inside, and the size and condition of a male influences who will be such holders (ie: larger males can hold larger nests and females prefer large males; eg: gobies).

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[7] "If the construction has no function for rearing offspring, but it is solely used for mate attraction and spawning, it is not a nest, but a bower" (Svensson and Kvarnemo 2023 p2).

Nest-site shortage means males who have no nest site of their own may be spawn parasitically (ie: sneaker male strategy). male sand gobies, for example, build sand burrows with small nest openings in the presence of sneaker males. This is a behaviour responding to sperm competition, which in externally fertilising fishes occurs after gamete release but before fertilisation. Smaller sneaker males may be able to access nests (a "dwarf male strategy" seen in some cichlids). Other strategies include isolated sites, or the use of biochemicals in the nest. "In gobies, the male prepares the spawning substrate with an anti-microbial mucus. The same mucus can also promote the fertilisation success of the nest holder, as it contains embedded sperm that activate gradually as the mucus dissolves" (Svensson and Kvarnemo 2023 p8).

Male three-spined sticklebacks with higher cognitive abilities build more elaborate nests, for example, and this is a clear advertising of "good quality" genes. Experimentally, it has been found that "females with medium-to-low cognitive ability prefer males with high ability, whereas females with high cognitive ability show no preference, suggesting greater benefits for females with medium-to-low than high cognitive abilities" (Svensson and Kvarnemo 2023 p5).

The next important characteristic is nest type, and Svensson and Kvarnemo (2023) distinguished the following among ray-finned fishes:

i) Elaborate (geometric circles, mounds and ridges) - eg: the white-spotted pufferfish builds a two metre-wide structure (ie: twice body length) in the sand consisting of circles and radial valleys. The male cares for the eggs laid within and maintains the structure.

ii) Burrows - eg: gobies, jawfishes, and catfishes dig in the substrate often under an object. A narrow entrance, for example, protects against predators, but also "enables the male force the female to spawn by preventing her from escaping" (Svensson and Kvarnemo 2023 p6).

iii) Bowls - These are shallow depressions in the substrate (sometimes under objects).

iv) Use of plants and algae - eg: some species of sticklebacks.

v) Use of animal matter - eg: some cichlid species build nests of empty gastropod shells.

vi) Self-produced nesting material - eg: glue, mucus, bubbles.

6.2.1. Cognitive Flexibility

"It has commonly been assumed that nesting behaviours are performed in a stereotypical and predictable manner, often without any prior experience or practice. For example, some bird parents retrieve an object close to their nest even if the object is not an egg, as long as it is similar enough to trigger the response" (Lehtonen et al 2023 p1). Though this is true for some species, Lehtonen et al (2023) argued that other species show cognitive flexibility in nest-building (eg: learning; problem-solving).

Cognitive flexibility can be seen in the different aspects of nest-building:

i) Nest site selection - For example, older female common eiders (Somateria mollissima) have greater nesting success because they have learned from previous experience about safe/unsafe sites. Other species show evidence of thinking ahead: "cliff swallows (Petrochelidon pyrrhonota) choose nest locations that are closer to nesting materials and sites that allow building of less time-consuming nests, thus suggesting that these birds are making initial decisions based on minimising the time and energy they later need to invest in nest construction" (Lehtonen et al 2023 p2).

Social learning is another cognitive ability. For example, European pied flycatchers (Ficedula hypoleuca) choose nest sites where species (tits) have been observed to have large clutches.

ii) Nesting material choice - "Learning can also allow nesting individuals to improve their nesting material selection. In zebra finches (Taeniopygia guttata), previous experience was found to influence nesting material choice: birds learned to prefer stiffer strings as a nest building material, thereby using fewer strings for a nest and increasing their nest building efficiency. Hence, the birds seem to learn to choose suitable nest material based on its suitability for a physical task, implying sophisticated 'physical cognition' [Bailey et al 2014]" (Lehtonen et al 2023 pp2-

3).

Evidence of innovation is seen in the use of human materials in nest-building (eg: plastic string by great grey shrikes (Lanius excubitor).

iii) Nest construction and nest architecture - "Laboratory rats (Rattus norvegicus domestica), for example, built more elaborate nests as adults if allowed to interact with nesting material as juveniles, implying that learning from prior experience allowed the rats to improve their nest building. Similarly, young village weaverbirds (Ploceus cucullatus) first build crude, loose structures for nests, whereas older individuals construct much more neatly woven, compact and organised nests, presumably reflecting learned weaving skills" (Lehtonen et al 2023 p3).

iv) Nest defence - This involves strategies to reduce nest predation like concealment or camouflage. "For instance, some species, such as hawksbill (Eretmochelys imbricata) and leatherback (Dermochelys coriacea) turtles, scatter sand away from their nest to create decoy trails to deliberately misguide would-be egg predators as to the location of the actual nest" (Lehtonen et al 2023 p4).

6.2.2. Nest Temperature

Nest temperature has long-term effects on the individual animal, particularly for ectotherms. Examples include Yucatan banded geckos and lower activity as an adult if raised in high incubation temperature, and adult bearded dragons faster at completing a social learning task if incubated at a cold temperature (De Jong et al 2023).

De Jong et al (2023) studied the delicate (or rainbow) skink (Lampropholis delicata) (figure 6.1) at three different incubation temperatures - cool (22 °C), mild (26 °C), and hot (30 °C). A number of measures were taken over the lifespan - while juveniles (4-6 weeks old), sub-adults (200 days old), and adults (two years old). Approximately twenty eggs were used in each of the three experimental conditions.

Sprint speed over one metre, for instance, varied with incubation temperature over the lifespan in that hot-incubated skinks were slower than mild-incubated individuals, who were slower than cool-incubated ones. Other measures were not so clear-cut. Growth rates, for

(Source: Xander T; public domain)

Figure 6.1 - The delicate skink.

example, were lowest in the mild temperature group, while resting metabolic rate was higher after cool incubation.

De Jong et al (2023) concluded: "Overall, our results demonstrate that incubation temperature can have lasting effects on later life stages, highlighting the importance of maternal nest-site selection, but that some effects are age dependent" (p1).

6.3. EVOLUTION OF NEST CHARACTERISTICS

Contact incubation used by birds, for instance, is where the incubator's body keep the eggs warm (known as thermoregulatory contact incubation), while crocodiles, for instance, bury their eggs. Deeming (2002) observed: "Presumably contact incubation in birds evolved from a habit of burying and guarding eggs" (quoted in Hogan and Varricchio 2023).

Using dinosaur fossil records, Hogan and Varricchio (2021) argued for two evolutionary antecedents - "that of weak contact incubation (contact incubating partially buried eggs...) and indirect contact incubation (whereby an endothermic adult provides energy to its fully buried clutch through the substrate medium that separates them)" (Hogan and Varricchio 2023 p2).

Domed nests built in cavities may have been the type of nest of the ancestors of modern passerines ("perching birds", which make up approximately 60% of avian species) (Ocampo et al 2023). "Dome nests (ie: nests constructed with roofs) are thought to provide substantial protection from the environment and predators, but they also restrict breeding opportunities and potentially limit a species' ecological niche. Open cup nests, on the other hand, are considered easier to build than dome nests and thus potentially facilitate the colonisation of new niches" (Ocampo et al 2023 p2).

Habitat is potentially key in the evolution of nest architecture, and Ocampo et al (2023) investigated this across 466 species of Tyrannida (tyrant flycatchers and allies - eg: mankins; sharpbills). Nests were categorised as cup or dome, and scored for location (branch, hanging, ground, banks, rocks, or cavity). Habitat type was divided into three: "closed (dense habitats in forest), semi-open (forest edges, dense understory, thickets or shrubland), or open (deserts, grassland, low shrubs, rocky habitats, seashores and cities)" (Ocampo et al 2023 p3).

Ocampo et al (2023) summed up their analysis: "The Tyrannida ancestor probably built a cup nest in a closed habitat, and dome nests independently evolved at least 15 times within this group. Both cup- and dome-nesting species diversified into semi-open and open habitats, and we did not detect a co-evolutionary relationship between nest type and habitat. Furthermore, nest type was not significantly correlated with several key ecological, life-history and environmental traits, suggesting that broad variation in Tyrannida nest architecture may not easily be explained by a single factor" (p1).

Also referring to ancestors, Mainwaring et al (2023b) pointed out: "The nests of euornithine birds - the precursors to modern birds - were probably partially open but the neornithine birds - or modern birds - were probably the first to build fully exposed nests" (p1). These researchers suggested that the evolution of open cup nests occurred as "best able to provide a location in which to raise altricial offspring". Such offspring are highly dependent on their parent(s) during the early stages of their lives, being born naked, blind, and helpless. "Open cup nests therefore provide more exposed conditions for parents and offspring but open cup nesting species protect themselves from adverse environmental conditions by adaptively using materials that provide insulation" (Mainwaring et al 2023b).

6.3.1. Beak Morphology

The beak is the chief appendage that birds use in nest building, though the feet and body are also used by some. The evolution of beak shape and size has been studied in relation to diet, for instance, but Sheard et al (2023) considered these characteristics and the evolution of nest characteristics.

Data on nest materials and beak traits from nearly 6000 species of birds were assessed. Nest material was categorised into seven groups - binder (eg: mud, sand, saliva), fibre (eg: feathers, fur), filamentous grass-like material (eg: grass, moss, kelp), leaf, mineral (eg: shells), silk, or twig (including bark). Each species was rated for their primary material. Four dimensions of beak size and shape were distinguished - total bill length, bill length from the nares (openings of the nasal cavities), bill width at the nares, and bill depth at the nares.

Statistical analysis showed that there was some relationship between beak morphology and nest material used. "For example, while grass is used by birds with many different beak sizes and shapes (other than small, pointy ones), silk is generally only used by small-billed species (of any width/depth:length ratio), and binder is generally only used by species with especially bulky bills (of any size)" (Sheard et al 2023 p6). But other variables were also important, for example, species diet, and access to materials, while heavier birds can carry heavier materials. Also the materials chosen "might be driven, for example, by sexual selection or by selection for particular thermal or anti-predator properties" (Sheard et al 2023 p6).

The beak is used in many ways by the bird, and so different selection pressures will be working upon it, for example, related to diet and foraging, and song (Sheard et al 2023).

6.3.2. Intra-Specific Variations

One "oversimplistic" classification of nests into several types is "open caps or domed nests built inside or outside cavities" (Perez et al 2023 p2). Perez et al (2023) commented: "The view that nest building is an instinctive and inflexible behaviour has led to a systematic disregard of variation in nest architecture within species, but it is now acknowledged that information from the environment and experience can affect nest building decisions" (p2).

Using a museum nest collection, Perez et al (2023) investigated intra-specific variation in nest morphology. They studied 745 nests from fifty-five species of birds kept at the National History Museum in the UK. Nest measurements were converted into a standardised score.

Other measures of a species were amassed, including behavioural flexibility, type of nest, body size, clutch size, and one or both parents responsible for nest building.

The species with the highest variability in nest characteristics differed by 20% or more on the standardised score compared to low variability species (with less than 2% difference between individuals). There was more variation in nest characteristics between individuals of the same species where single parents built the nest, where there was a large variation in clutch size, and for domed nests than open cup nests. However, nest building flexibility is not linked to behavioural flexibility" (Mainwaring et al 2023a p3).

6.3.3. Ants

"In ants, variation in nest architecture reflects both differences in ecology and in the collective behaviour of the colonies that live in the nests. Each component of the nest (such as depth, and the number, size and connectivity of chambers) reflects selective pressures for different functions, or structural constraints that are imposed by the environment or evolutionary history" (O'Fallon et al 2023 p1).

O'Fallon et al (2023) compared forty-two nests of two closely related species (Dorymyrmex bureni and Dorymyrmex elegans) in Florida to understand the selective pressures. These are ground-dwelling species that dig nests in the soil. Data from a literature review were also used for information on other related species.

The characteristics of the nests were scored - depth, number of chambers, width of entrance chamber, and network density (eg: number of connecting tunnels). Foraging strategy was also scored (table 6.1).

There were significant differences between the species on total nest depth, number of chambers, network density, and entrance chamber width. Foraging strategy was a good predictor of nest characteristics in statistical models. For example, "species in which foragers recruit nestmates to food have larger entrance chambers, which potentially allow for more efficient recruitment, compared to species that use solitary or stable trail foraging strategies. In solitary foraging, there is no recruitment. When there is an established foraging trail, foragers can recruit nestmates to new food directly from the stable trail rather than, or in addition to, from inside the nest. Thus, species that

- Solitary - ants leave nest individually and do not interact during food search.

- Group recruitment - a forager returns to nest with food and recruits others to return to food source.

- Stable trails - foragers leave the nest and follow trails previously created.

- Mass recruitment - a forager returns to nest with food and recruits a large number of others to follow pheromone trail created.

Table 6.1 - Foraging strategy of ant species.

employ solitary or stable trail foraging strategies likely do not require large spaces at the entrance of the nest to recruit nestmates to food. Instead, they can maintain smaller entrance chambers that potentially reduce the risks imposed by invading competitors" (O'Fallon et al 2023 p8).

Other differences included that solitary forager species had less deep nests, and less number of chambers compared to ants that employed mass foraging and stable trails foraging.

6.4. LARGE COMMUNAL NESTS IN HARSH ENVIRONMENTS

The Namib Desert is very arid (with 10 mm of rainfall on average per year in the most arid parts) (Juergens et al 2023). It is home to "fairy circles" - circular bare patches of sandy soil lacking plant cover surrounded by a ring of tall grass hassocks. They were first documented scientifically in the 1970s, and the main hypotheses include toxic substances from dead shrubs, geochemical gas, self-regulation by plants, and sand termites (Psammotermes allocerus) (Juergens et al 2023).

Jurgens (2022) used five time-lapse videos to show the germination and death of grasses after rainfall in such a way that it was evidence of sand termite nests beneath the soil. "The central bare areas of fairy circles serve the key function of storing moisture received from sparse rainfall. The sandy soil texture allows rapid infiltration and percolation of precipitation, while localised herbivory by the termites creates the bare patch, thereby reducing the rapid loss of soil moisture by the uptake and transpiration of water by plants. The resulting storage of rain water even during prolonged periods of drought enables perennial life in hyper-arid desert environments and forms a globally unique example of ecosystem engineering by social insects" (Juergens et al 2023 p1).

6.5. NESTS TODAY

Many bird species use anthropogenic nest materials (ANMs) (eg: sweet wrappers; cigarette butts; plastic strings; fragments of plastic bags). The presence of ANMs were observed in the early 19th century with the first published report in the 1930s. However, the use has increased dramatically in recent years (Jagiello et al 2023).

For example, Hartwig et al (2007) found that around 40% of over 450 black-legged kittiwake nests in a colony in Denmark in 1992 contained ANMs, but this had risen to nearly 60% of over 300 nests there in 2005 (Jagiello et al 2023).

Jagiello et al (2023) outlined the main hypotheses for the use of ANMs by birds:

i) "Availability" - birds use the materials in the local environment.

ii) "Age" - older birds use more ANMs (ie: learning from past experience).

iii) "New location" - the use of new sites (ie: human-related, like chimneys) limits the choice of non-ANMs.

iv) "Signalling" - ANMs are chosen to signal to potential mates the quality of the nest builder (eg: bowerbirds).

Jagiello et al (2023) performed a literature review to test the above hypotheses. They found 75 relevant academic articles on ANM use by 176 species. A number of variables about each species were also collated (eg: bill length; nest type; sex of nest builder).

The most common ANM used was plastic (string/rope; foil/sheet; thread; hard plastic; bags), followed by cloth, and paper. "This finding is not surprising given that plastic is one of the main anthropogenic synthetic substances with a current production reaching 348 million tonnes per year or that global estimates indicate that the majority (79%) of all plastic ever produced persists in the environment to this day, and thus is environmentally available" (Jagiello et al 2023).

The ANM used varied with the environment (marine; urban terrestrial; non-urban terrestrial). "In marine environments, a wide range of fishing gear such as rope, string, fishing line, mesh, netting and lobster pot tags , and other plastics such as food wrapping, plastic bags, cords and sheets were documented in birds' nests. In terrestrial environments that are heavily modified by humans (eg: urban areas) ANMs included cotton threads, plastic broom fibres, paper, sweet wrappers, cigarette butts, polyethylene, paper towels, wet wipes, synthetic cotton, dental floss and bottle labels" (Jagiello et al 2023).

Support was found for sexual signalling (eg: bright colours), as well as benefits in terms of anti-parasite (eg: nicotine in cigarette butts), and strengthening the nest structure. The main costs were risk of entanglement (eg: 6% of American crow nestlings in 195 nests; Townsend and Barker 2014), and ingestion (eg: rubber bands in gut of dead white storks; Henry et al 2011). The bright colours of ANMs may also attract predators. ANMs may improve thermal regulation of the nest, or cool quicker than natural materials, depending on the study (Jagiello et al 2023) (table 6.2).

There was some support for the availability hypothesis, none for the age hypothesis, and the evidence was unclear about the new location hypothesis (Jagiello et al 2023).

COSTS	BENEFITS
1. Entanglement. 2. Ingestion. 3. Health risk (eg: nicotine from cigarette butts; pathogen on ANM). 4. Reduce nest temperature. 5. Attract predators via artificially bright colours.	1. ANMs better than natural materials for nest building. 2. Increased nest temperature. 3. Sexual signalling. 4. Anti-parasite (eg: nicotine). 5. Repel predators (eg: nicotine).

(After table 3 Jagiello et al 2023)

Table 6.2 - Main costs and benefits of birds using ANMs in nests.

6.6. ELABORATE NESTS

Street et al (2022) began: "The structural complexity of birds' nests varies enormously across species, from roughly constructed stick platforms to neatly woven cups and domes" (p1). These researchers pointed out that, perhaps, "the most complex of all birds' nests are 'pendent' designs — enclosed domes dangling precariously from substrates above, resembling hanging-baskets" (Street et al 2022 p1) (figure 6.2). Weaverbirds and icterids are the best examples of pendant nest builders, and they "must knot, stitch and weave together hundreds of strips of nesting material, requiring a significant amount of physical effort, manipulative skill and trial-and-error learning. Such nests, therefore, presumably confer substantial fitness benefits to compensate for the costs of their construction" (Street et al 2022 p1). The advantage is probably in relation to snake predators, and brood parasites.

(Source: Jim Conrad; public domain)

Figure 6.2 - An oriole (icterid) nest.

However, not all weaverbirds and icterids build such complex nests, with some species not building nests but using those built by others. Complex nests evolved independently in these two families of birds. Street et al (2022) made the following prediction: "If elaborate structural features of pendent nests provide protection from nest invasion by arboreal predators or brood parasites, then species building more protected nests, ie: those with tunnels and/or with more precarious attachments, should show evidence of reduced offspring mortality compared with species that build less protected nests" (p2).

The researchers collected data on weaverbird (56 species) and icterid (n = 48) species (eg: yellow-headed blackbird). Nests were categorised based on two dimensions - the presence of entrance tunnels, and the type of attachment (supported, suspended or pendulous). Street et al (2022) explained: "We classified as 'supported' nests those that are attached from the underside to a branch, built on the ground or firmly attached on two sides between vertical supports rising up from the ground. We classified as 'suspended' nests attached at the top or side(s), so that the bulk of the nest lies below the substrate, while we classified 'pendulous' nests as those hanging from the substrate above by a single point of attachment" (p3). Nest location was also categorised - in thorny vegetation, over water, in large breeding colonies, or close to nests of aggressive stinging insects or predatory birds.

Firstly, it was found that weaverbird species "building nests with entrance tunnels have offspring with slightly longer combined developmental periods [incubation and nesting periods] than those building nests without entrance tunnels" (Street et al 2022 p4). Nest location had no impact on developmental period length. The type of attachment did not vary the developmental period length, but among icterid species it did matter. "Icterid species building pendulous nests (which incorporate upward-facing tunnels) have longer developmental periods compared with those building suspended nests, who in turn have longer developmental periods than those building supported nests" (Street et al 2022 p7).

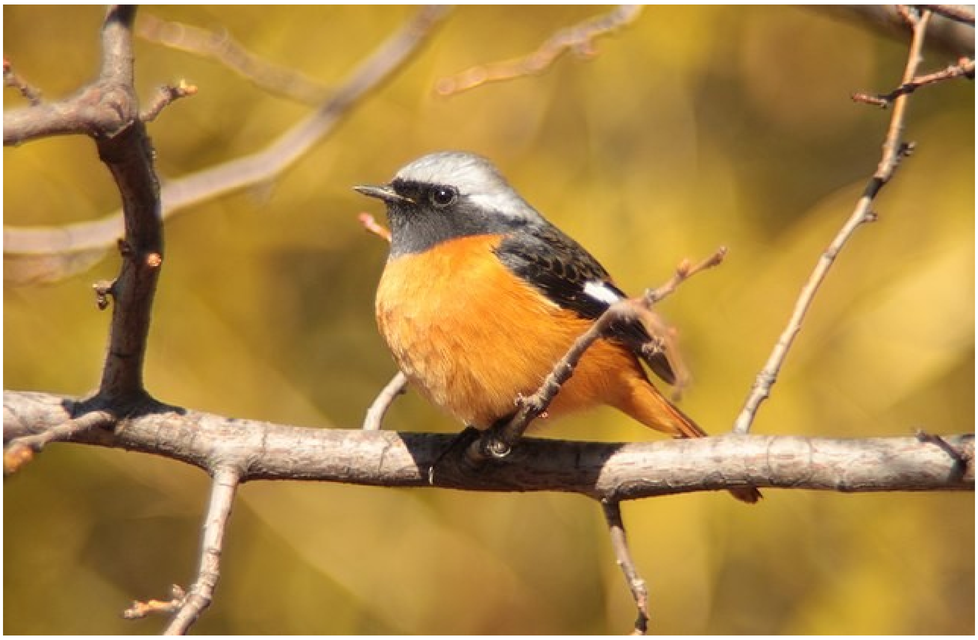
A longer developmental period is seen in species across the animal kingdom under lower predator pressure and/or with less risk of brood parasites. So, it is possible to draw the conclusion that elaborate nests evolved with the advantage of lower offspring mortality outweighing the cost of building them.

An entirely different strategy to combat brood parasitism is to nest near to humans. Zhang et al (2023) showed this advantage in Daurian redstarts (Phoenicurus auroreus) (figure 6.3) (host) and the common cuckoo (Cuculus canorus) (brood parasite).

These researchers used both observational data from north-eastern China, and experimental work. The former included 490 nests over four breeding seasons (2018 to 2021), of which 15% were parasitised overall. "Nests outside a building were about three times more likely to be parasitised by a cuckoo than nests inside a building. Moreover, for outdoor nests, the probability of parasitism increased with increasing distance to the nearest building" (Zhang et al 2023 p1125).

Also redstarts have two egg-laying periods, of which only one is at risk from cuckoos. it was observed that "redstarts adjusted their nesting location in response to a seasonally predictable change in the risk of brood parasitism" (Zhang et al 2023 p1125). Twice as likely to nest inside a building in the period when cuckoos present than when absent.

Experimentally simulating the presence of cuckoos (when they were naturally absent) increased the likelihood of nest indoors or closer to human settlements.



(Source: pcs34560; public domain)

Figure 6.3 - Daurian redstart.

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7. VETERINARY ANTHROPOLOGY

7.1. OVERVIEW

"Veterinary anthropology" (VA) "studies the participation of animals in meaning-making processes about notions such as life, health, birth, disease, and death, using its own methods of investigation" (Broz et al 2023 p2). It is a collaboration between veterinarians and anthropologists, and Broz et al (2023) distinguished three areas of particular interest:

i) Risk - This is in relation to zoonoses (ie: diseases that jump from non-humans to humans). The focus is upon the social and cultural practices that increase such risks. For example, in Hog et al's (2021) study of live poultry markets and avian influenza in Chattogram, Bangladesh, "retailers are not free agents calculating the benefits and risks of reporting sick poultry, but rather, they follow structural constraints that determine their everyday life and gestures" (Broz et al 2023 p3) (table 7.1) (appendix 7A).

- Hog et al (2021) explained: "Trade in 'sick' birds follows a tendency: It is easier to sell asymptomatically infected birds as 'healthy birds', because it is impossible to identify the infection. It is more difficult to sell visibly sick birds to city markets. Yet, trade in sick birds is ongoing, because a small profit is better than no profit. Visibly sick birds are sold to local shops, local markets, hotels, restaurants and social event agencies on average 40 per cent of the market price. 'Apparently healthy birds' are those that are suspected to be infected, as they have been in a flock of visibly sick birds eventually with a degree of mortality. Middlemen and feed dealers sell sick birds for three reasons: lack of storage and treatment facilities, to maintain good relations with the farmers and to avoid losing money. Farmers have economic reasons for selling sick birds" (pp9-10).

- A "credit farmer" called "Amon" said: "I try my best to treat the sick birds before selling. If the birds do not recover and selling time comes, then I sell the sick birds mixed with the healthy birds to the feed dealer. I know it is unethical to sell sick birds, but I have no other choice but to sell them to minimise my economic losses to at least get a little bit of profit" (p10).

- "Credit farmers" take a loan to buy the chicks, and then pay it back from selling the adult birds. "Farmers are under pressure to sell sick birds, facing the choices of negative, zero or marginal profit. They have no other choice but to act in their own rather than in the general interest. From their perspective, they act rationally – in economic terms. Reactive behaviours, based on constrained choice, points to actions of last or only hope. The individual's ability to act independently to escape the determinism of the structural constraints is limited. This is about constrained agency in their everyday farming lives" (Hog et al 2021 p10).

- This behaviour takes place within conditions called a "risk environment": "A risk environment for exposure to infectious diseases delineates social, physical, economic and policy contexts in which a variety of factors exogenous to the individual interact to promote the adoption of risky practises, increasing the chance of harm occurring. Such focus on risk environment stems from the idea that social structures determine individual practise, simultaneously recognising that a risk environment is a product of the inseparable interplay between micro-, meso- and macro-level factors. In other words, there can be several types of interacting and overlapping risk environments in a given context" (Hog et al 2021 p2).

Table 7.1 - Limited agency and "sick" birds.

ii) "Animals in infrastructures" - For example, "the animal turn in anthropology" has been used to describe "viewing animals as agents interacting with humans in fundamental dimensions of social life" (Broz et al 2023 p4). This includes different views of animals from the scientific gaze of the West to hunters in Amazonia who "must adopt the perspective of the animals they prey on, treat them as kin, and ask for their consent. For Amazonian shamans, 'to know is to personify, in take the point of view of that which must be known' [de Castro 2004]" (Broz et al 2023 pp4-5). Put another way, to move from humans as the central figure and nature as the background.

iii) Anthropology of veterinarians - Exploring veterinary practices (specifically the dominance of the medical model) through the lens of anthropology.

7.2. RISK

Uganda is an example of a country where the commercialisation of agriculture has the potential as "a route out of poverty" (Arvidsson et al 2022 p2) for smallholders. "Pigs especially have attracted interest due to their short generation interval, minimal space requirement and rapid multiplication rates. However, their potential as a route out of poverty is limited by, among other things, disease and health problems. Smallholders have limited access to veterinary services, with the main providers often being paraprofessionals" (Arvidsson et al 2022 p2).

Paraprofessionals are individuals with a limited amount of veterinary training who work where qualified veterinary care is not available or too expensive. For example, they have general agriculture or animal management qualifications or short-term training from a non-governmental organisation (NGO).

The veterinary professionals tend to view the paraprofessionals as "quacks", and highlight the negative outcomes for animal health. But the "public veterinary sector is massively under-resourced; thus while inadequately trained paraprofessionals and insufficient veterinary support currently present a risks to animal health, paraprofessionals fulfil an important role for smallholders unable to access the public veterinary sector" (Arvidsson et al 2022 p1).

Broz et al (2023) noted a parallel with "duck doctors" in China (Fearnley 2020), who are "consulted by farmers to provide anti-biotics and anti-virals against poultry diseases, yet they are suspected to be cheaters or quacks by official veterinarians who practice surveillance for avian influenza and report cases to the authorities. These 'duck doctors' are closer than official veterinarians to the different scales of poultry farming, from big industrial farms to small poultry farms. Small poultry breeders, often mixing wild and domestic poultry, contend that small scale farming produces a form of immunity toward avian influenza, which, in their view, only affects big industrial farms" (p4).

Such false beliefs and the knowledge gaps of paraprofessionals heighten the risk of zoonoses. Arvidsson et al (2022) concluded that "both animal health and smallholders' livelihoods would benefit from closer collaboration between veterinarians and paraprofessionals and from a better understanding of smallholders' needs" (p1).

7.3. ANIMALS IN INFRASTRUCTURES

Desmond (2022) considered the relationship between veterinary medicine and clinical medicine, with particular reference to the USA: "Veterinary clinical medicine is both like and strikingly unlike human medicine in crucial ways. Certainly, there are deep similarities. Lab animals serve as research subjects to develop medicine for human benefit. Certain techniques are developed on animals prior to translation into human treatments. At the cellular level, for some species at least, basic biological processes are the same. And sometimes animals benefit from treatments that first become widespread for humans, as in the newer applications of radiological treatments for cancers in dogs. But in practice, what can appear so similar on the surface, from the white coated doctor to the MRI [magnetic resonance imaging] machine, is actually different from human medicine in almost every dimension from diagnosis to treatment to finances to ethics to technology" (p3).

She continued: "The mere presence of the modifier 'veterinary' added to the word medicine, indicates the secondary nature of the field. Even the US professional degrees are marked in this way... A DVM, is a Doctor of Veterinary Medicine. An MD is simply a 'medical doctor', not a Doctor of Human Medicine. The categorical distinction is also a hierarchical one, echoing the secondary status of animals vis a vis humans, and it has impacts on every dimension of clinical practice" (Desmond 2022 p4). This "binary frame" of human/animal medicine suggests a clear and absolute dividing line between human and non-human patients, but Desmond (2022) stated, "we know that this is not true. Instead the line of demarcation between the human and non-human realms is historically and culturally shaped, contextually invoked, and differentially impactful in distinct realms of practice, including scientific, religious, or spiritual or imaginative and artistic realms" (p4).

An example of the context can be seen in the different categories of US veterinary medicine - production medicine (dealing with animals raised for food), companion animal medicine (eg: cats and dogs), equine medicine (ie: horse-related), and exotic/wildlife/zoo medicine (Desmond 2022). "Differential valuations according to human categories of use and affection forcefully shape the medical starting points and outcomes for individual animals" (Desmond 2022 p5). More literally, this is seen in the amount of money humans are willing to spend on the treatment of the animal. "No one with a life threatening medical situation arriving at the emergency room of a human hospital can be turned away simply because they lack insurance. They will at least receive basic assistance even if not granted access to the most elaborate regimes of care... Veterinarians can legally turn away animals brought into their clinic — for example, a dog found by the side of the highway — if the person bringing that animal in cannot pay" (Desmond 2022 p5).

Other differences between human and animal medicine include the many different species treated by veterinarians, and the ability to offer euthanasia to suffering animals, while not being able to ask the patient how the injury occurred.

The resistance towards human vaccination that has grown in the 21st century has also occurred with companion animal vaccines. Hobson-West's (2022) analysis of online pet vaccine critical materials found "a similar discursive form to organised critique of childhood vaccination. For scholars keen to break down barriers between the study of human and animal medicine, this finding should not be seen as surprising. Afterall, 'vaccines are vaccines', whatever species their recipient: The fundamental questions of risk, trust in expertise and imaginaries of science are clearly not unique to human medicine" (p5).

Hobson-West (2022) distinguished three strands of argument used by human and animal vaccine resistance groups:

i) A reframing of risk - "In summary, risk is framed as either unknown, because of the claim that insufficient monitoring of disease and vaccine adverse reactions is done in the veterinary field; concealed, in that those in positions of authority such as veterinarians are not sharing what they do know; or is framed as non-random" (Hobson-West 2022 p4). The latter point relates to the idea that individuals can control health risks through diet, for example.

ii) Not to have "blind trust" in the veterinary (or medical) profession.

iii) The collection of their own data by vaccine resistance groups.

7.4. ANTHROPOLOGY OF VETERINARIANS

Ashall (2020) used her experience of euthanising a dog as a newly qualified veterinary surgeon to explore ethnography (and auto-ethnography) in VA, and a feminist ethic of care (Gilligan 1993). Ethnography involves the use of participant observation (ie: observing by being part of the observed group), and auto-ethnography is observing the self in this situation. So, a veterinary surgeon observing the profession from within.

After describing the case of the dog (table 7.2), Ashall (2020) explained: "I describe my feelings of relief that I had ended the dog's suffering and my absolute certainty that I had done the right thing by ending its life. I knew that she was too unwell to recover and was suffering to such a great extent that immediate euthanasia was my only option. I did the only thing that I could do as a veterinary surgeon, for an animal under my care. I am satisfied that my actions met my professional obligation to have regard first to animal welfare. However, the story also tells how this case ultimately left me feeling confused and uncertain about where the boundaries of my professional responsibility lay. Whilst I had absolute certainty about what I should do for the animal itself, I was very much less certain about my handling of the surrounding situation. What else should I have done? How could I prevent this happening again? Why did I feel so unhappy?" (p9).

This raises ethical questions, which are assumed will be addressed in a rational and logical way. But the lived experience of the veterinary surgeon is an emotional one, and a feminist ethic of care accepts that ethical decisions in real-life cannot be divorced from the moment [8]. "Our emotions are also important, ... [Mullan and Fawcett 2017] argue, for empathetic responses to the needs of another" (Ashall 2022 p6).

Also such an approach takes account of wider factors (ie: "the politics of care"). "A veterinary feminist care approach might provide a framework for redefining the focus of veterinary professional responsibility, beyond the health of animals and toward the maintenance of healthy relationships between humans and animals" (Ashall 2022 p12).

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[8] Gilligan (1993) talked of 'a mode of thinking that is contextual and narrative, rather than formal and abstract' (quoted in Ashall 2022).

- "I can still see the dog's face as its eyes connected with mine, framed by the black bin bag it had been carried in. I can still hear the clicking sound, louder than the animal's shrill cries, made by a mass of maggots moving against one another beneath the dogs matted fur, moistened by fluids leaking from its damaged flesh. My hands were shaking with panic and rage and I could hardly draw up the euthatal into the syringe quickly enough. I wanted to put an end to this, immediately. As the lethal fluid flowed into the tiny vein the dog's body finally relaxed. At my hand, like so many others, she had ceased to exist. Through the window I could see her owners waiting outside in the sunshine to pay me and I thought about the silky feel of the fur which covered an expensively shaped head. I knew this dog was loved once" (Ashall 2022 p1).

Table 7.2 - Euthanising a dog as a newly qualified veterinary surgeon.

From another ethical standpoint, Chao (2022) considered the issue of animal ethics and halal slaughter in Islam. "When killing animals for food is conducted, the slaughter must be done in the name of God as a sacred ritual in order to assure that the life of the animal is not taken lightly and that the slaughter is not a sign of hostility toward the universe. Before the act of sacrifice, the animal must be healthy, and no harm should be forced upon it. Accordingly, the requirement of pre-slaughter stunning has posed a question to Muslim scholars: Does stunning kill the animal or cause harm? What defines harm, and whose definition counts?" (Chao 2022 p1). Veterinary anthropology can help to resolve such questions in finding common ground between secular and Islamic views. Data were collected in Malaysia and New Zealand.

7.5. APPENDIX 7A - AVIAN INFLUENZA

Elsmo et al (2023) reported evidence of the "highly pathogenic avian influenza virus" (HPAIv) H5N1 in sixty-seven wild terrestrial mammals (eg: red fox; ferret; Eurasian lynx) throughout the USA in 2022. Infected mammals showed neurological symptoms. Some of the data came from post-mortem studies, and the rest from live observations. The latter provided evidence of the live symptoms (eg: seizures; tremors; lethargy). Ingestion of infected wild birds was assumed to be the source of disease for the mammals.

Neurological symptoms mean that the virus has invaded the central nervous system, but the cells here are different to those in the respiratory tract, the normal site of infection in birds. Viral adaptation to cells in the central nervous system requires an evolution of the virus. Siegers et al (2023) experimentally inoculated ferrets with the HPAIv to investigate the possibility of evolution of the virus to survive in the mammalian central nervous system. The study showed that the HPAIv could enter the central nervous system via the olfactory nerve, and adapt to survive therein (eg: in the brainstem).

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8. FIRST REPORTS AND RARE BEHAVIOURS

8.1. TORPOR IN SWIFTS BUT NOT NESTING HUMMINGBIRDS

To save energy, some animals can reduce their body temperature and metabolism, and go into a state of torpor. Among birds, for example, hummingbirds can reduce their metabolic rate by over 90% on a daily basis (Wellbrock et al 2022). It is a strategy to deal with food shortage and/or cold temperatures (appendix 8A).

The common swift (Apus apus) has been studied in the laboratory, where food and water deprivation, and/or environmental temperature can be controlled. Body temperature and metabolic rate were reduced (Wellbrock et al 2022).

Wellbrock et al (2022) reported the first study of free-living common swifts nesting in Germany and torpor. Data were available for a colony of up to 55 breeding pairs in 2010-15 and 2017-18. Measures were made of nest temperature, and gas exchange (to show metabolic rate), as well as video recordings, in selected nests in 2017-18.

Six nocturnal torpor events were observed and measured, during which the metabolic rate was reduced by around half and body temperature by about 7 °C.

Maintaining the appropriate nest temperature for eggs can be a challenge for mothers who have to balance their energy intake and expenditure in relation to their own survival. "For small animals that rely on the limited amount of energy stores to survive periods of food unavailability, such as hummingbirds, it may be especially difficult to maintain consistently warm nest temperatures while sustaining their own energy balance" (Eberts et al 2023 p1).

One response observed in hummingbirds is night-time torpor (appendix 8B). However, this is rare in the breeding season by mothers. "At night, the mother relies on the limited amount of energy that she stored during the day to maintain a normothermic metabolism and warm nest temperatures... While she could enter torpor to survive if she depletes her energy reserves to critically low levels, doing so could delay the development of her thermally sensitive offspring" (Eberts et al 2023 p2).

Eberts et al (2023) collected data on free-living nesting female Allen's hummingbirds (Selasphorus sasin) in California using thermal imaging cameras. Eye temperature was used as the measure of internal body temperature because of the low feather density, and four states were categorised - sleep (normothermy) (high and stable eye temperature), deep torpor (low and stable temperature), shallow torpor (immediate temperature), and transition to and from torpor (changing eye temperature). Of 67 active nests, 56 were monitored until the offspring fledged, were preyed upon (eg: by American crows), or were abandoned. A total of 108 nights in 2017 and 2018 were recorded. Only 5% of these were not classified as normothermy (two clear cases of deep torpor and three of shallow torpor).

Night-time nest temperature is crucial, and so mothers needed to not be in deep torpor (low body temperature and consequently low nest temperature). The mothers employed strategies like extra-feeding in the evening to maximise fat deposits for the night, or building thick and well-insulated nests. The latter would also reduce the need for torpor (at least in mild weather conditions). The deep torpor cases were observed after rainy days when the female had not been able to feed, but stayed at the nest to protect the eggs from water. There were too few cases to make generalisations (Eberts et al 2023). Also cases of shallow torpor may have been missed.

Eberts et al (2023) concluded: "We found that Allen's hummingbird females rarely enter torpor, a key energy-saving adaptation that defines Trochilidae, while nesting. Instead, females seem to employ alternative strategies, including an insulative nest and possibly shallow torpor, to reduce their own energy requirements while prioritising the energetic demands of their offspring" (p6).

8.1.1. Appendix 8A - Hibernation More Generally

The common ancestor of all mammals probably hibernated. "The idea that ancient humans could hibernate may seem far-fetched, but mounting evidence suggests that many non-hibernating mammals retain an ability to enter reduced-energy states, including through dormant brain-signalling pathways that slow metabolism" (Wilkins 2022 p47).

Hibernation is based around a state of torpor, which can vary between animals (eg: number of degrees of drop in body temperature), and in length (eg: hours to weeks). "What's more, some hibernators regularly come in and out of torpor into states of arousal, while others stay metabolically suppressed" (Wilkins 2022 p47).

A continuum of hibernation is one way to understand it, from the thirteen-lined ground squirrel that can last in a state for six months (with successive cycles of torpor and arousal, and little body temperature drop), while, at the other end, black bears lower their body temperature and metabolism drastically (Wilkins 2022).

One element of thermoregulation is brown adipose tissue activation, which is increased by cold and inhibited by heat. The opposite is "thermoregulatory inversion" (Tupone et al 2017). This process appears to occur in hibernating or torpid mammals, for example, which "reduce their metabolism and energy consumption to cope with cold environmental challenges" (Tupone et al 2017 pR783).

8.1.2. Appendix 8B - Andean Hummingbirds

Hummingbirds living at high elevations in the Andes are an example of avian adaptation to extreme environments. "The challenges of living in these cold, wet and hypoxic environments are compounded by hummingbirds being among the smallest of endotherms and possessing the highest mass-specific metabolic rates of any vertebrates. Pronounced thermoregulatory costs are combined with very high costs of hovering flight at high elevations and a diet of flower nectar requiring daily intake rates sometimes exceeding hummingbirds’ own body masses" (Wolf et al 2020 p1).

Certain strategies are used, including roosting in warm caves, intense feeding before dark, and nocturnal torpor. Body temperature is reduced by 10-30 °C in the latter case (Wolf et al 2020).

Wolf et al (2020) studied six species of hummingbird (n = 26 individuals) living at over 3000 m above sea level in Peru (table 8.1). The study took place in March (2015) when there is approximately twelve hours of darkness and twelve of light.

All species in the study entered nocturnal torpor, but the length varied (from around 2 to 13 hours in the most extreme individuals), as did the minimum body temperature (as low as 4 °C at one extreme, and in the mid-30s °C at the other). Recovering from deep torpor was surprisingly rapid. Overnight energy loss was negatively related to length of torpor bout.

Common Name	Latin Name	Number of individuals studied	Average duration of torpor (hrs)
Giant hummingbird	Patagonia gigas	4	5.70
Black metaltail	Metallura phoebe	5	10.61
Bronze-tailed comet	Polyonymus caroli	1	12.95
Black-breasted hillstar	Oreatrochilus melanogastar	4	6.45
Shining sunbeam	Aglaeactis cupripennis	7	5.91
Sparkling violetear	Colibri coruscans	5	6.18

Table 8.1 - Six species of hummingbird studied by Wolf et al (2020) and average duration of torpor.

In similar research, Shankar et al (2022) used thermal imaging to detect nighttime body temperature of thirty-three hummingbirds (from three species - Rivoli's and black-chinned hummingbirds, and blue-throated mountain gems). A variety of strategies were used, from normal sleep (with body temperature 1-2 °C below resting day-time temperature) to shallow and deeper torpor (2-20 °C below daytime) (Burke 2022).

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8.2. TRANSITION TO SIBLINGHOOD STRESS

"Most children are exposed to the birth of a younger sibling while still being dependent on parental support. For the older offspring, this transition to siblinghood (TTS) marks the onset of considerable changes, including the sudden emergence of a competitor (sibling rivalry...) and a decline in maternal investment" (Behringer et al 2022 p3). Thus, TTS is seen as a stressful life event. It is well studied in humans (eg: Volling 2012), but Behringer et al (2022) investigated TTS in bonobos (Pan paniscus).

The inter-birth intervals ranged from 2.3 to 8.6 years in the study population, which meant that older siblings varied from highly dependent to more independent. Urinary cortisol was used as the measure of TTS stress, which was expected to increase at sibling birth (ie: increased stress).

A five-fold increase in urinary cortisol levels was found, and a high level continued for about seven months after sibling birth. Age at TTS did not influence the findings.

Certain behaviours were observed prior to the sibling birth and afterwards which created the TTS. These included time suckling, riding on the mother, and body contact decreased, while time spent foraging independently increased.

Putting the increase in cortisol in context, captive bonobos in an experimental stress test had a two-fold increase, while wild chimpanzees encountering a neighbouring group had an increase of one and a half times the normal level (Behringer et al 2022).

The study population was wild bonobos of the Bompusa West and East communities at LuiKotale, Democratic Republic of the Congo. They are well studied, and so habituated to human presence. Urinary cortisol was measured from 26 individuals by opportunist collection from vegetation.

This study, the researchers claimed, was "the first to investigate the physiological stress response during TTS" (Behringer et al 2022 p10).

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8.3. INTER-SPECIFIC ALLOPARENTAL CARE

The interactions between killer whales (Orcinus orca) and long-finned pilot whales (Globicephala melas) have been observed in the North Atlantic Ocean, including predation and chases. There are not many reports, and they seem to be resource competition (Mrusczok et al 2023).

Mrusczok et al (2023) reported the first documented account of a group of killer whales appearing to care for a lone long-finned pilot whale, seen on 12th August 2021 near Iceland. This was "a form of inter-specific alloparental care" (Mrusczok et al 2023 p289). The observation lasted twenty-one minutes, and the calf appeared "emaciated". The calf was not observed nursing. The researchers did not see how the relationship began nor what happened subsequently to the calf.

"In mammalian species, it is thought that individuals caring for non-descendant young may acquire selective advantages such as parental experience or reciprocal altruism" (Mrusczok et al 2023 p289). Also the alloparent may have recently lost a newborn or had a near-term miscarriage, and so be lactating. "Alloparental care between killer whales and pilot whales may be possible because of the similar long-term co-operative group structure and mother-offspring relationships in both species" (Mrusczok et al 2023 p290).

Inter-species alloparental care has been reported in delphinid species before (eg: short-beaked common dolphin; common bottlenose dolphin) (Mrusczok et al 2023).

Reference

Mrusczok, M-T et al (2023) First account of apparent alloparental care of a long-finned pilot whale calf (Globicephala melas) by a female killer whale (Orcinus orca) Canadian Journal of Zoology 101, 288-293

9. COMMUNICATION AND SIGNALS

9.1. LOUD CALLS OF HOWLER MONKEYS

Howler monkeys produce complex, loud, long low-frequency calls, which are "unique among the platyrrhines" (Kitchen et al 2015 p371). But these animals are mostly inactive, due in large part to a folivorous diet that produces little energy, so why do they "invest so much time and effort into loud calling" (Kitchen et al 2015 p371)?

The function of loud calls in the animal kingdom can be categorised as (Kitchen et al 2015):

i) To maintain group cohesion - eg: contact calls during travel or when separated. A small number of studies noted some evidence of this in howler monkeys. For example, around one-third of male brown howler monkeys (Alouatta guariba) howling bouts occurred during separation from the group (Steinmetz 2005 quoted in Kitchen et al 2015).

ii) To reduce predation risk (ie: alarm calls) - Kitchen et al (2015) commented that "the rarity of predator encounters observed by humans" (p372) makes it difficult to say definitively. Calling has been reported in predator encounters as well as silence.

iii) To attract, and bond with males - For loud calls to be a sexual signal, Snowdon (2004) proposed five criteria - "signals must be (1) sexually dimorphic, (2) variable among males, (3) discriminated among individuals, (4) preferred or avoided in context of reproductive access, and (5) related to increased reproductive fitness" (Kitchen et al 2015 p372). All these criteria have been established in howler monkeys, though the last one has weaker evidence (Kitchen et al 2015). As males are calling mostly, then female choice of mate has an influence on the production of loud calls (ie: selection pressure).

iv) To compete with other individuals - This is evidence that loud calling regulates space in the forest between different groups (ie: a means of defending territory). It is a way to settle territorial disputes without chases and fights.

Loud calling as territorial defence would predict differences in behaviours depending on the part of the territory/home range (ie: centre or border). For example, calling in response to simulated intruders (with playback recordings) was greater in the centre than the border area (Kitchen et al 2015).

Loud calling as defence of females, and infants (as infanticide is a risk) has been reported in some studies (Kitchen et al 2015).

Females also produce loud calls, but to a lesser extent than males, and particularly to the dominant male. Sekulic (1983) proposed a number of hypotheses for the specific function of female loud calls:

a) To incite male competition - "However, this predicts that females should call first, which rarely happens in howler monkeys; in fact, it is more likely that the male's incipient roars, usually uttered at the onset of roar bouts..., can act as a recruitment call, prompting other group members to join in the roar chorus... Moreover, Sekulic's hypothesis suggests that males are in a state of constant intra-group competition, another unlikely assumption. It is also unclear why males should need female loud calls as incentive to compete" (Kitchen et al 2015 p386).

b) To intimidate females from other groups - There is limited evidence that solitary females evoke female calling, but more likely by both sexes.

c) To encourage the dominant male to protect her offspring - Infanticide is a risk if a new male takes over the group. There is some evidence of female loud calling as a means to bond with the dominant male.

da Cunha and Byrne (2006) added the hypothesis that female loud calling is supportive of males in territory defence. There is support for this idea in a playback experiment that found that mantled howler monkey (Alouatta palliata) groups were more likely to move in response to combined male and female roars than just male roars (Whitehead 1989).

There are other variables in the function of loud calls, including the time of the day, and that calls have different functions within a population as compared to between populations. There are a number of different species of howler monkey (12; Youlatos et al 2015).

References

da Cunha, R.G.T & Byrne, R.W (2006) Roars of black howling monkeys (Alouatta caraya): Evidence for a function in inter-group spacing Behaviour 143, 1169-1199

Kitchen, D.M et al (2015) Function of loud calls in howler monkeys. In Kowalewski, M.M et al (eds) Howler Monkeys: Adaptive Radiation, Synthesis, and Morphology New York: Springer

Sekulic, R (1983) The effect of female calls on male howling in red howler monkeys (Alouatta seniculus) International Journal of Primatology 4, 291-305

Snowdon, C.T (2004) Sexual selection and communication. In Kappeler, P.M & van Schaik, C.P (eds) Sexual Selection in Primates: New and Comparative Perspectives Cambridge: Cambridge University Press

Whitehead, J.M (1989) The effect of the location of a simulated intruder on responses to long-distance vocalisations of mantled howling monkeys, Alouatta palliata palliata Behaviour 108, 73-103

Youlatos, D et al (2015) New challenges in the study of howler monkey anatomy, physiology, sensory ecology, and evolution: Where we are and where we need to go? In Kowalewski, M.M et al (eds) Howler Monkeys: Adaptive Radiation, Synthesis, and Morphology New York: Springer

9.2. VOCAL ACCOMMODATION

Vocal learning is the ability to modify one's vocalisations (eg: birds learning new songs from conspecifics). But for species that do not show vocal learning, there is a "halfway house" of "vocal accommodation" (ie: some adaptation of calls in response to environmental conditions, like increasing loudness in noisy environments) (Baciadonna et al 2022).

Baciadonna et al (2022) investigated vocal accommodation in the calls of African penguins (Spheniscus demersus) at a marine park in Italy. Audio recordings and behavioural observations were made of three colonies between 2014 and 2017, and in 2020.

Fourteen acoustic parameters were analysed (eg: fundamental frequency; amplitude modulation rate and duration).

There was evidence that some of the call parameters were similar for members of the same colony, which suggested that contact calls were "modified subtly in response to their social environment over long periods of time" (Baciadonna et al 2022 p4).

The researchers continued: "Ecological pressures of colony life pushes for vocal accommodation to help identify and discriminate colony mates from penguins outside the colony. We speculate that, similar to what has been found in monkeys [Fischer et al 2020], vocal accommodation may help clusters of penguins within the same colony identify each other" (Baciadonna et al 2022 p6).

Fischer et al (2020) had found that "the acoustic structure of male baboons' calls was found to be more similar between males that spent more time together even when genetic relatedness was taken into account. These results and similar findings suggest that even when a primate is not capable of explicit vocal learning, their vocalisations can be modified in response to social interactions. In particular, the more pairs of individuals experience each other's calls, the more their calls change to sound similar" (Baciadonna et al 2022 p2).

References

Baciadonna, L et al (2022) Vocal accommodation in penguins (Spheniscus demersus) as a result of social environment Proceedings of the Royal Society B 289, 20220626

Fischer, J et al (2020) Vocal convergence in a multi-level primate society: Insights into the evolution of vocal learning Proceedings of the Royal Society B 287, 20202531

9.3. EVOLUTION OF ACOUSTIC COMMUNICATION

The evolution of acoustic communication in vertebrates could have occurred in one of two ways - evolved independently multiple times in different species (over thirty times; Jorgewich-Cohen et al 2022) (ie: convergent evolution) as shown by the variety in production and reception physiology, or "has a common and ancient evolutionary origin" (Jorgewich-Cohen et al 2022).

Jorgewich-Cohen et al (2022) favoured the latter because "vertebrate hearing epithelia and cerebral promotor circuits that control vocal behaviours are considered to be homologous and operate in the same hindbrain compartment, respectively. Furthermore, in spite of the variety of sound production mechanisms, all Choanata (Dipnoi (lungfishes) + Tetrapoda) lineages have lungs as the physical source of their calling behaviours" (p1).

These researchers collected audio recordings data on fifty-three species of Lepidosauria (lizards and snakes), non-anuran Amphibia (eg: salamanders), Chelonians (turtles), and lungfishes (Dipnol) thought to be non-vocal. importantly, acoustic abilities were evident in several species considered non-vocal. Along with information on other similar species (from a dataset compiled by Chen and Wiens 2020), phylogenetic comparative analyses were performed to construct a family tree to a common ancestor that lived over 400 million years ago.

References

Chen, Z & Wiens, J.J (2020) The origins of acoustic communication in vertebrates Nature Communications 11, article 369

Jorgewich-Cohen, G et al (2022) Common evolutionary origin of acoustic communication in choanate vertebrates Nature Communications 13, article 6089

9.4. VOCAL RANGE OF BATS

"The evolution of powered flight, echolocation, and subsequent fast buzzing allows bats to hunt and capture fast-moving airborne prey and thereby exploit the riches of the night: flying insects. To detect small prey, biosonar signals need to contain high frequencies to provide efficient acoustic reflection and high bandwidth to provide high localisation accuracy and spatial resolution" (Hakansson et al 2022 p1). This was one selection pressure on the evolution of laryngeal structures.

But bats also make social communication calls at lower frequencies, and this evolved via different selection pressures. Hakansson et al (2022) argued that "different selection pressures for echolocation and social communication facilitated the evolution of separate laryngeal structures that together vastly expanded the vocal range in bats" (p1). Overall, the frequency range spans 1 to 120 kHz (6-7 octaves) (while humans and other mammals typically only produce three octaves and in exceptional cases four to five"; Hakansson et al 2022 p2), and echolocation calls can last 1-2 msecs in duration (Hakanssen et al 2022).

The vocal folds of bats show several adaptations compared to mammals generally, and the combination of different laryngeal structures produces the vast frequency range. Hakansson et al (2022) studied Daubenton's bat (Myotis daubentonii) with a range of 1 to 95 kHz.

Reference

Hakansson, J et al (2022) Bats expand their vocal range by recruiting different laryngeal structures for echolocation and social communication PLoS Biology 20, 11, e3001881 (Freely available at https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.3001881)

9.5. CO-SPEECH SIGNALS

Human speech is combined with gestures, body movements, and facial expressions in the everyday use. These "co-speech signals" are "presumably a way to enhance communication" (Aychet et al 2021 p203).

Aychet et al (2021) studied the different signals of 25 captive red-capped mangabeys (Cercocebus torquatus) (figure 9.1) housed at a university in France. Over fifty hours of observations in 2018 recorded three types of signals - "body signals", "facial signals", and "vocal signals" (table 9.1) - which combined into 424 communication sequences that could be grouped into eight categories (eg: aggressive; affiliative). "Overall, captive mangabeys frequently associated communication signals of all types (body, facial and vocal signals) and modalities (visual, audible and tactile), in a flexible way" (Aychet et al 2021 p203).

The findings fit with the "multi-modal theory" of human language evolution, "which advocates that human language emerged from the co-evolution of gestural, vocal and orofacial communication in the primate lineage under different ecological and social constraints" (Aychet et al 2021 p215).

SIGNAL TYPE	SUB-TYPE	DEFINITION
Body	Head movements Bang object	Shake head: "Signaller moves his/her head with quick repeated movements, horizontally or vertically". "Signaller jumps on cage wall or perches after having taken a run-up or grabs and shakes cage wall or perches (with hands only or with hands and feet), producing tremors and noise".
Face	Bite self Lipsmack	"Signaller bites herself/himself or an object, staring at the receiver". "Signaller sticks out his/her tongue and moves it between the lips with rapid repeated movements".
Vocal	Sexual call Alarm call	"Oe" vocal unit. "WaHoo" call.

(Source: Table 3 pp209-210 Aychet et al 2021)

Table 9.1 - Examples of three types of signals.

(Source: Altalpanther; public domain)

Figure 9.1 - Two mangabeys.

Reference

Aychet, J et al (2021) Sequential and network analyses to describe multiple signal use in captive mangabeys Animal Behaviour 182, 203-226

9.6. HOMEOACTIVE SENSING

Self-directed signal production (or homeoactive sensing) is used in spatial navigation. Bats, for example, emit high-pitch calls as a means to locate stationary and moving objects from the echo (ie: echolocation) (Oboti et al 2023).

The brown ghost knifefish (Apteronotus leptorhynchus) does a similar thing with weak electric signals (ie: electrolocation) (Oboti et al 2023).

Reference

Oboti, L et al (2023) Why the brown ghost chirps at night bioRxiv (https://www.biorxiv.org/content/10.1101/2022.12.29.522225v4)

9.7. BADGE OF STATUS

The "badge of status" hypothesis (Rohwer 1975) "predicts that individuals use signals, such as colour ornaments, to assess social dominance or fighting ability of others, thus diminishing the need for aggressive interactions to settle disputes" (Beltrao et al 2021 p240). This is the case with plumage colours in birds.

Beltrao et al (2021) reported that among the common waxbill (Estrilda astrild) red colour patches on the breast predicted social dominance above other signals like body size. The birds were observed in a large semi-natural environment near Porto, Portugal around feeders (between 2017 and 2019). Dominance in interactions was measured by the response of the feeding individual when another individual approaches. There is potential for conflict here, but an already existing dominance hierarchy will resolve this risk. In other words, an arriving dominant individual will automatically displace a subordinate feeding, but not vice versa. Dominance hierarchies require clear signals (or badges of status) as in red colour patches here.

Beltrao et al (2021) had different findings to work on waxbills in birdcages (eg: Funghi et al 2015), where body size was associated with dominance. The researchers explained that "we studied waxbills interacting mostly when in the air, around feeders placed over 1 m high on a wall, whereas in birdcages they had little room to fly and interacted mostly on perches or on the cage floor. Waxbills are very light (ca. 8 g) and acrobatic, and in nature they mostly feed perched on the stems of grasses..., so that most of their interactions occur in the air. Larger weight or body size may confer fighting advantages when animals interact on the ground, but not necessarily in aerial interactions" (Beltrao et al 2021 p246).

9.7.1. Cost and Honesty

Ornaments and other signals need to be honest (ie: poor quality individuals cannot fake them), and the "physiological cost hypothesis" proposes that "endogenous constraints, such as energetic..., oxidative... or immunosuppressive... costs incurred during signal production or maintenance limit an individual's signalling ability" (Welklin et al 2021 p173). In other words, the cost of producing the signal can only be incurred by good quality individuals, and is thus an honest signal.

An example of a well-studied species is the red-backed fairy-wren (Malarus melanocephalus), where males acquire ornamental plumage for the breeding season. "In fairy-wrens, moult into ornamented plumage involves replacing all feathers but the wing feathers and is typically followed by an increase in courtship behaviour that continues throughout the breeding season... Combined, moult and courtship are thought to be physiologically intensive..." (Welklin et al 2021 p174). Welklin et al (2021) investigated this in a colour-banded population in Queensland, Australia, in 2015-2019. Males were rated for highest plumage score into three groups - brown, intermediate, and red-black (ornamented plumage). The timing of ornamented plumage acquisition was recorded.

All males three years and older acquired ornamented plumage (n = 105), as did nearly all two year-olds (n = 112 vs 5), but only a minority of one year-olds (n = 52 vs 162 brown). Whether the males acquired ornamented plumage and the timing of doing so varied with age. The one year-olds were more likely to acquire the plumage if they already had a mate at the start of the breeding season in an area with few neighbours, while others remained in brown plumage in crowded areas and/or who were unpaired (ie: social cues). "This indicates that the benefits of ornamented plumage - namely increased reproductive success... - may outweigh the costs only when males are likely to obtain a breeding role in an uncrowded environment, or that males are constrained from obtaining ornamented plumage after the start of breeding"

(Welklin et al 2021 p181). But older males were influenced by environmental cues like rainfall, with drier non-breeding seasons leading to poorer physiological condition (and later timing of moult). This fits with the physiological cost hypothesis for older males, whereas for younger males "social cues appear to play a larger role than abiotic environmental factors in determining ornament acquisition" (Welklin et al 2021 p173).

References

Beltrao, P et al (2021) Plumage colour saturation predicts long-term, cross-seasonal social dominance in a mutually ornamented bird Animal Behaviour 182, 239-250

Funghi, C et al (2015) Social dominance in a gregarious bird is related to body size but not to standard personality assays Ethology 121, 84-93

Rohwer, S (1975) The social significance of avian winter plumage variability Evolution 29, 593-610

Welklin, J.F et al (2021) Social and abiotic factors differentially affect plumage ornamentation of young and old males in an Australian songbird Animal Behaviour 182, 173-188

10. MATING AND SOCIAL BEHAVIOURS

10.1. GUARD VS SNEAKER MALES

Males of the same species may employ different mating strategies (known as "alternative reproductive tactics"; ARTs). For example, large-horned male taurus scarab beetles guard tunnel entrances wherein females live, while short-horned or hornless males dig adjoining tunnels to "sneak" access to females (Synyshyn et al 2021).

Differences in behaviour during the mating season (eg: aggression/guarding; "sneaky") may be evident outside the mating period (ie: consistent behavioural traits). Synyshyn et al (2021) investigated this possibility in the round goby (Neogobius melanostomus) (figures 10.1 and 10.2), which has two male ARTs - nest-guarding, and nest-sneaking.

(Source: Yavno; public domain)

Figure 10.1 - Round goby (guard male).

Males caught in the Laurentian Great Lakes, USA, were tested in the laboratory for behavioural tendencies - exploration/boldness (in a new environment), sociality

(Source: US Fish and Wildlife Service; public domain)

Figure 10.1 – Round goby (sneaker male).

(choosing to be alone or near other males), and aggression (towards a mirror image) (table 10.1). The males were categorised as guards or sneakers based on size and colour. "Males designated as guarder males (GM) were black or extremely dark, had wide heads and were generally larger... Males classified as sneaker males (SM) were lightly mottled, had narrow heads, were typically smaller..." (Synyshyn et al 2021 p229).

Differences were found between the two categories of males, with SM being more explorative and bold, and less aggressive than GM. The GM behaviour was more consistent, "suggesting that sneaker males might be more behaviourally plastic" (Synyshyn et al 2021 p227).

BEHAVIOUR	EXPERIMENT SET-UP	MAIN FINDING
Exploration	An individual fish was placed inside a refuge in a new tank, and after a period of habituation, a door is opened allowing movement into the tank. The willingness of the fish to leave the shelter in 15 minutes was scored, along with time taken to leave, and the amount of movement within the tank based on a 4 x 4 grid on the tank floor.	i) 8 of 25 GM never left the refuge compared to 3 of 40 SM. ii) No difference in average time taken to leave for those who left the refuge. iii) SM explored more of the tank.
Sociality	A tank divided into different sections by clear perspex with the test individual at one end and three males at the other end. The test male could choose to move into a section near the males ("social zone") or move away ("asocial zone").	There was no difference in the time spent in the social zone between GM and SM.
Aggression	An individual male is placed in a tank and a mirror is unveiled, so he sees "a perfectly size-matched 'competitor conspecific'" (p229). Aggressive behaviour (eg: rams; parallel displays) measured for 30 minutes.	There was no difference, but the GM performed significantly more aggressive acts in the social zone in the above experiment.

Table 10.1 - Details of the main experiments by Synyshyn et al (2021).

Reference

Synyshyn, C et al (2021) Non-mating behavioural differences between male tactics in the invasive round goby Animal Behaviour 182, 227-237

10.2. RELATIONSHIP QUALITY

Socially monogamous species may pair-bond for a season or over several seasons. The latter (long-lasting pair-bonds) can mean the maintaining of the relationship during the non-breeding period. This is not well studied (Maldonado-Chaparro et al 2021).

Maldonado-Chaparro et al (2021) investigated this topic with captive-bred zebra finches (Taeniopygia guttata) in large outdoor aviaries in Germany over two years (2017 and 2018). All birds were identifiable, and the whole environment was covered by video cameras. The quality of pair-bond relationship was scored based on time spent interacting during the pre-breeding season.

Three key issues were studied related to the quality of the relationship - likelihood to breed, reproductive performance (eg: clutch size; time to lay first clutch), and probability of divorce. Data on 127 breeding pairs were used.

There was variety in the process of bond formation, but generally "pairs that developed stronger and more stable social relationships outside the breeding season were more likely to breed together and form a pair bond. Moreover, pairs that formed a stable social relationship initiated reproduction faster than those with less stable pair bonds, while the stability and the length of time since establishment of the pair bond both reduced the probability of divorcing" (Maldonado-Chaparro et al 2021 p43).

So, maintaining the pair-bond relationship outside the breeding season has its advantages. Maldonado-Chaparro et al (2021) observed that "zebra finches breed opportunistically... in response to rainfall patterns, which in their natural habitat are unpredictable... Maintaining pair bonds, even outside the reproductive season, might provide adaptive benefits such as reduced predation and increased breeding performance and fitness... Continuous pair bonding also allows pairs to initiate a clutch faster (ie: fast-track hypothesis; Adkins-Regan and Tomaszycki 2007), providing a reproductive advantage when conditions become suitable for breeding" (p44).

References

Adkins-Regan, E & Tomaszycki, M (2007) Monogamy on the fast track Biology Letters 3, 6, 617-619

Maldonado-Chaparro, A.A et al (2021) Relationship quality underpins pair bond formation and subsequent reproductive performance Animal Behaviour 182, 43-58

10.3. SEXUAL COERCION

Sexual coercion is the "use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile [direct coercion], and to decrease the chances that she will mate with other males [indirect coercion], at some cost to the female" (Smuts and Smuts

1993 quoted in Kunz et al 2021).

There is the direct form of sexual coercion as in forced copulation, where the male uses "superior speed or strength to catch and physically restrain a female while he copulates with her by force" (Clutton-Brock and Parker 1995 quoted in Kunz et al 2021). This is more common in invertebrates. The other form of sexual coercion is indirect, as in harassment and intimidation, common in social mammals (Kunz et al 2021).

Variables in the use of sexual coercion by males include dispersed females, concealed ovulation, shortage of females, and a strategy by subordinate males (Kunz et al 2021).

Kunz et al (2021) concentrated on orang-utans, "so far the only non-human primate, and maybe even mammal, genus where forced copulations are frequently reported" (p68). Long-term data were available (2003 to 2018) from two reserves in Indonesia, including nearly 500 observed copulations. Female resistance or non-resistance was scored in each case, along with variables like the presence of other males within fifty metres.

Overall, 103 copulations were classed as resisted and 71 as non-resisted for analysis purposes. In summary, Kunz et al (2021) found that "the males' decision to coerce and the females' decision to resist were highly context dependent" (p75).

The use of sexual coercion by males could be called a "now-or-never" tactic - ie: it was "most likely to occur on days with other males in the vicinity, and thus when males were at risk of losing access to a female" (Kunz et al 2021 p75).

The female behaviour of resistance or not could be called a "not-you-now" tactic - ie: "they resisted mating with subordinate males especially if more dominant males were in the vicinity but mated with them voluntarily at other times. Females were less likely to resist mating initiations with dominant males who displaced other males" (Kunz et al 2021 p75). The researchers argued that the female behaviour fitted with the "infanticide avoidance hypothesis" (Hrdy 1979). This includes the idea of "paternity confusion" here, and Kunz et al (2021) explained that "females are expected to be selectively promiscuous to achieve the optimal balance of paternity assessments among the males in the area, including potential fathers refraining from attacking infants and possibly providing protection. This is what the results of our current study indicate: females appear to tolerate copulations with subordinate males for paternity dilution purposes in the absence of more dominant males. Yet, if a more dominant male is in the vicinity, females resist mating with the current male, and thus signal their unwillingness to mate with a subordinate male to the dominant male, and thereby increase the dominant male's assessment of his paternity chances" (p77).

The researchers continued: "Although direct evidence for the occurrence of infanticide remains elusive in wild orang-utans..., female orang-utans certainly meet the criteria to be vulnerable to the conception-hastening effect of infant loss..., with their slow life history including the high lactation to gestation ratio... and their solitary lifestyle.... In the absence of permanent associations, which could provide protection against infanticidal attacks..., female orang-utans have evolved efficient sexual and behavioural counter-strategies which make infanticide generally unprofitable for males, as the latter cannot reliably monopolise sexual access to females" (Kunz et al 2021 p77).

References

Clutton-Brock, T,H & Parker, G.A (1995) Sexual coercion in animal societies Animal Behaviour 49, 1345-1365

Hrdy, S.B (1979) Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females Ethology and Sociobiology 1, 13-40

Kunz, J.A et al (2021) The context of sexual coercion in orang-utans: When do male and female mating interests collide? Animal Behaviour 182, 67-90

Smuts, B.B & Smuts, R.W (1993) Male aggression and sexual coercion of females in non-human primates and other mammals: Evidence and theoretical implications Advances in the Study of Behaviour 22, 1-63

10.4. SOCIAL COMPETENCE

“Social competence” involves maximising social interactions in group-living animals. For example, rewarding individuals who rewarded you in the past, and not those who did not. So, individuals should adjust their behaviour to interact more with those who are most rewarding.

Kings et al (2023) investigated this behaviour in an experiment with wild jackdaws (Corvus monedula). The experiment involved a feeder with two compartments (one containing low quality food (grain) and the other high quality food (mealworm)). The behaviour of one jackdaw in a pair influenced the food reward of the second. The conditions were varied such that one jackdaw received low quality food while the other high quality food, or both the same or nothing. Subsequently, these radio frequency identification tagged birds were observed to see who they interacted with during social foraging. There was evidence of preference for individuals associated with high reward, but the effect was small. This suggested that "individuals are likely to forego potential short-term benefits to retain associations with valuable long-term partners" (Kings et al 2023 p6).

This makes sense because jackdaws are "highly social, colony-breeding corvids that form long-term, strictly monogamous pair bonds. Offspring retain close, prolonged associations with their parents post-fledging, and siblings from the same brood commonly associate together in creches and at foraging sites. Jackdaws co-operate with other colony members to deter predators and engage in social foraging with both kin (ie: siblings, parents and their offspring) and non-kin, often forming large flocks that exhibit fission–fusion dynamics" (Kings et al 2023 p2).

Reference

Kings, M et al (2023) Wild jackdaws can selectively adjust their social associations while preserving valuable long-term relationships Nature Communications 14, article 5103

10.5. SEXUAL CANNIBALISM AND PRAYING MANTIS

Sexual cannibalism involves "attacking and consuming a prospective or realised mate" (Pollo et al 2021 p1). Pre-copulatory sexual cannibalism occurs in the springbok mantis (Miomantis caffra) where females attack males. But not all encounters are like this, so are there individual differences between the females who attack and do not attack, and the males who do or do not become victims?

Pollo et al (2021) investigated these questions with juvenile mantises caught in New Zealand. Thirty-five females were scored for aggressiveness based on speed of catching flies, and 39 males for activity (based on amount of movement). Then thirty-five mating trials were performed.

The pair interacted in eighteen trials, and in thirteen of these there was pre-copulatory sexual cannibalism. Successful mating occurred in the other trials.

Pollo et al (2021) summed up the findings: "Females that were aggressive as juveniles were not more likely to cannibalise males when adult following physical interaction, but males made physical contact with these females sooner and more often. More active males were both faster and more likely to interact with females, but were not more likely to be cannibalised in the process. We also found that female age influenced sexual interactions: younger females were more likely to cannibalise males. Taken together, our results suggest that both male and female personality influence the likelihood of sexual encounter, but have little effect on the likelihood of cannibalism" (p1).

The "aggressive spillover hypothesis" (Arnqvist and Henriksson 1997) was not supported. This is a theory based on sexual cannibalism in spiders, which states that "aggressiveness that is advantageous in a foraging context (towards prey) when females are developing may 'spill over' to the mating context (towards conspecific males) in the adult stage" (Pollo et al 2021 p2).

References

Arnqvist, G & Henriksson, S (1997) Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints Evolutionary Ecology 11, 3, 255-273

Pollo, P et al (2021) Effects of male and female personality on sexual cannibalism in the springbok mantis Animal Behaviour 182, 1-7

10.6. SOCIAL SELECTION

"Social selection" (West-Eberhard 1983) is a process by which individuals of the same species compete for resources, and the more successful survive and reproduce. "Besides competing for mates, conspecific individuals also socially compete for other resources such as food and territories, driving the evolution of social traits such as ornaments (conspicuous decorative traits...), weaponry (eg: horns) and behaviours (eg: song) that mediate access and defence of those resources..." (Macedo et al 2021 p1).

A result of this can be sexual dichromatism, as in birds, where the male and female of the species have different colouration. Studying the different antbird species, Macedo et al (2021) noted differences in the amount of sexual dichromatism. These researchers tested experimentally the territorial behaviour of males and females in more or less sexually dichromatic species in Brazil. Antbirds are socially monogamous, and both partners defend the territory.

Playback recordings were used to simulate a territorial intrusion by a solitary female, a solitary male, or a pair. The behaviour of the territory owners was measured (eg: approaching and singing; agonistic behaviours). "Agonistic behaviours include changing perches frequently in short flight bursts and/or hopping vigorously on the forest floor while producing harsh alarm calls, arching their backs and ruffling their feathers to make their bodies look bigger, spreading and repeatedly flicking their tails and displaying interscapular plumage patches that usually remain hidden" (Macedo et al 2021 p112).

Males of all colouration responded to all intrusions in the same way, but females reacted differently depending on the colouration of the species. Females of species with more conspicuous colouration (eg: ochre-rumped antbird; Drymophila ochropyga) responded more strongly than females of species with less conspicuous appearance (eg: rufous-tailed antbird; Drymophila genei), but only to solitary intruders. The researchers interpreted the findings as evidence of female colouration as reflecting social selection. Put another way, conspicuous colouration is "a signal of competitive ability in females" (Macedo et al 2021 p119).

References

Macedo, G et al (2021) Differences in plumage colouration predict female but not male territorial responses in three antbird sister species pairs Animal Behaviour 182, 107-124

West-Eberhard, M.J (1983) Sexual selection, social competition, and speciation Quarterly Review of Biology 58, 2, 155-183

11. MOVEMENT

11.1. TERRESTRIALITY

The evolutionary transition of primates from living in the trees (arboreality) to on the ground (terrestriality) involves costs and benefits including greater predation risk on the ground, but easier movement over longer distances, and it can be cooler than than the upper canopy. The latter is important in extreme heatwaves, particularly with the availability of water on the ground. Species-specific factors like diet, and form of locomotion may also be relevant (Eppley et al 2022).

Eppley et al (2022) analysed data on forty-seven arboreal primate species in the Americas and Madagascar around time spent on the ground, and the factors associated with it. In total, 150 961 observation hours over 2227 months at sixty-eight research sites (twenty in Madagascar). Time spent on the ground was positively associated with maximum monthly temperature, and negatively associated with habitat canopy (eg: size of uninterrupted forest). The shift to terrestriality was also influenced by a dietary shift from fruits (ie: more general diet), and larger group size. There was great variety in behaviour between the species, and overall time spent on the ground was less than 5% of total monthly activity.

Reference

Eppley, T.M et al (2022) Factors influencing terrestriality in primates of the Americas and Madagascar PNAS 119, 42, e2121105119

11.2. WALKING CATFISH

There are a small number of air-breathing fish, and so they are able to move on land. Some can survive for eighteen hours out of water, and move up to 1.2 km at a time on land (Bressman et al 2020).

One example is the walking catfish (Clarias batrachus) (figure 11.1), which is an invasive species in Florida. Bressman et al (202) studied 150 adults caught in that state in 2018 and 2019. The researchers were interested in the use of chemical cues to orient themselves on land.

In an experiment, a fish was placed in the centre of a terrestrial arena, and one of nine smells was released from a certain point. The fish responded positively towards alanine, and pond water, but away from hydrogen sulphide.

The researchers also surveyed 88 volunteers in Florida via relevant Facebook groups, and analysed thirty-eight YouTube videos. These observational data on walking catfish presented a picture of them appearing during and after heavy summer rain to feed on terrestrial invertebrates.

Bressman et al (2020) ended with these remarks: "As an ecologically harmful species that can spread to new bodies of water underground and overland, the urban-adapted C. batrachus is a particularly difficult invasive fish to manage. As an economically harmful species, they can cause substantial losses in ornamental fish farm ponds and frequent intervention can be required to remove these pests from such aquaculture facilities... However, we offer some potential solutions for reducing the ability to disperse. Terrestrial traps could be created using attractive volatile compounds for this species and placed near ornamental fish aquaculture facilities and yet uninvaded bodies of water to lure individuals away from the water itself" (p904).

(Source: Vassil; public domain)

Figure 11.1 - Walking catfish in an aquarium.

Reference

Bressman, N.R et al (2020) Why did the invasive walking catfish cross the road? Terrestrial chemoreception described for the first time in a fish Journal of Fish Biology 97, 895-907

11.3. TERMITES

There are around 3000 described species of the eusocial cockroach known as termites. They are divided into two families - Termitidae ("higher termites") and Kalotermitidae. The latter are more often invasive species, though with less diverse species (Bucek et al 2022) [9].

Though termites have winged alates (wing-like structures), they are poor flyers, and so their long-distance dispersal is probably by trans-oceanic rafting (ie: nesting in and feeding on pieces of wood). In latter years termites can live in the wood transported around the world by humans (Bucek et al 2022).

This can be seen in the case of Krakatau islands, defaunated by a volcanic eruption in 1883, but termites were found there in the late 20th century (Gathorne-Hardy and Jones 2000).

References

Bucek, A et al (2022) Molecular phylogeny reveals the past trans-oceanic voyages of drywood termites (Isoptera, Kalotermitidae) Molecular Biology and Evolution 39, 5, msa093

Gathorne-Hardy, F.J & Jones, D (2000) The recolonisation of the Krakatau islands by termites (Isoptera), and their biogeographical origins Biological Journal of the Linnean Society 71, 2, 251-267

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[9] In taxonomy, a Species is a sub-division of a Genus, and a Genus is a sub-division of a Family, while a Family is a sub-division of an Order.