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

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CONTENTS

1. SEXUAL CANNIBALISM

1.1. EXPLANATIONS

"Sexual cannibalism" (SXC) is "the consumption of a potential mate during or after courtship or copulation" (Baruffaldi and Andrade 2021 p1), and it is mostly the female who eats the male. This is also pre-copulation SXC.

A number of hypotheses have been proposed to explain its evolution, including (Baruffaldi and Andrade 2021):

i) It provides the mated female with nutrients which will benefit the offspring ("foraging strategy hypothesis") (eg: praying mantids; Barry et al 2008; appendix 1A). This explains pre-copulation, during and post-copulation SXC, and the latter two are reasons for males to accept it.

ii) It is a means of females controlling paternity (ie: male whose courtship is low quality is eaten). Better to explain pre-copulation SXC.

iii) Mistaken identity (eg: small males perceived as prey). Or it can be "the side effect of an increased foraging vigour of females that mature at a smaller size and body mass" (Barry et al 2008 p710).

vi) "Aggression-spillover hypothesis" - "aggressiveness, which is adaptive in juvenile phases, could be out of control in adults and maintained at non-adaptive levels" (Aisenberg et al 2011 p68).

v) Males may be complicit because it guarantees their paternity and/or success of their offspring. Does not explain pre-copulation SXC.

Males have evolved strategies to avoid being eaten, including short copulations, only mating with females eating prey, and autotomising of copulatory organ (ie: detaching it from the body and it continues to transfer sperm while the male escapes) (Baruffaldi and Andrade

2021) (appendix 1B).

Much of the research is with spiders. Baruffaldi and Andrade (2021) studied Latrodectus mirabilis (a species of black widow spider) in the laboratory. Mating was video recorded between an unmated male and an unmated female or a previously-mated female.

Of 21 unmated females, around two-thirds ended mating with SXC, and this was over 80% with the nineteen previously-mated females. "When sexual cannibalism occurred, it was usually during copulation, when the male's palp was inserted in the female genitalia" (Baruffaldi and Andrade 2021 p5). The researchers believed that this was "a unique form of sexual cannibalism not previously reported for the genus, with males cannibalised during sperm transfer as the result of the female behaviour" (Baruffaldi and Andrade 2021 p6).

What do males gain in this situation? The first male to mate with a female does not assure paternity because the females mate again after SXC. But if the chance of finding a female is low, then any mating opportunity is better than none, even if it ends in death.

1.2. MALE SEXUAL CANNIBALS

Reversed SXC is "very infrequent", and an "economic model" has been proposed - ie: males eat females when food is scarce (Aisenberg et al 2011).

Aisenberg et al (2011) considered other possibilities with the sand-dwelling wolf spider (Allocosa brasiliensis), which shows sex role reversal, and males larger than females. Males dig burrows and females search for mates. After mating, the female is sealed into the burrow until the eggs hatch, and she and the spiderlings emerge. The first mating of a virgin female produces the most eggs. A male must dig a new burrow for every mating opportunity, while the female only has to find another male and burrow. So, the males have a high reproductive investment, while favours them being the "choosy sex". So, "males may use cannibalism as a mechanism of mate choice, perhaps to avoid the cost of losing a burrow to a low-quality female" (Aisenberg et al 2011 p69).

Aisenberg et al (2011), thus, predicted that males will be more likely to cannibalise already mated females, and/or those in poor body condition. Spiders were captured from beaches in Uruguay (n = 45 adult males, 84 adult females, and 66 sub-adults).

Twenty males were chosen for the experiment, and each of them was placed in a sandy arena for 48 hours to allow burrow construction. Then they were consecutively exposed to a virgin and an already mated female (with 48 hours in between). The order was counter-balanced. Each trial lasted one hour, and was scored as copulation, cannibalism or neither.

The twenty males mated with nine virgin and three mated females, but attacked three virgins and eight mated females. "Body condition and weight were not related with cannibalism occurrence when virgin and mated females were compared separately. However, when both groups were compared together, a higher number of male attacks were registered on those females showing lower weights" (Aisenberg et al 2011 p71).

The findings were taken as support for the "extreme mate choice hypothesis" (Elgar and Nash 1988). "Males of A. brasiliensis showed sexual preference towards females with characteristics related to high reproductive success (ie: virgin and heavier females with higher body condition indices) and attacks were more frequent towards females that showed lower weight values. In spiders, higher weight and body condition index are associated with a higher expected fecundity, reflected, for example, by the number of eggs" (Aisenberg et al 2011 p72).

How the male is able to distinguish between a virgin and a mated female, the researchers could not say. No difference in courtship behaviour by the different females was observed. "Males could be able to detect volatile or contact pheromones belonging to the female or to her previous sexual mate, or detect silk cues released by spiderlings that had hung from the female dorsum; however, additional experiments are required on these topics" (Aisenberg et al 2011 p73).

In another spider, Micaria sociabilis, Sentenska and Pekar (2013) found SXC of older females. Captured spiders from three years in the Czech Republic were used in the experiment that released a male and female into a container. Four behaviours were scored - "classical" SXC (ie: female kills male), reversed SXC (male kills female), copulation, and none of the above within 20 minutes. In total, there were 121 males and 121 females used.

The body size of the spiders was varied only with the age (based on birth in spring or summer), and the female status of virgin or already mated.

No cases of classical SXC were observed, but reversed SXC occurred in around 20% of trials. Body size or mating status did not influence SXC by males. But Sentenska and Pekar (2013) found "the highest frequency of cannibalism during the period when young males from the summer generation met old females from the previous spring generation. This increased frequency of cannibalism of old females suggests male mate choice based on female age. In general, the number of oocytes in females is limited, and after its depletion females experience reproductive senescence" (p1136). So, older females can be classed as "low-quality mates" compared to younger females. Sentenska and Pekar (2013) continued: "we presume that males would do better to reject old females and wait for young ones from the new generation regardless of whether the ovaries of older females are depleted or not. Cannibalism during the period when two generations of M. sociabilis overlapped seems to be an advantageous strategy. By killing low-quality females from the previous generation, the cannibalistic males do not lose a valuable mating opportunity as females from the new generation are available within a few days" (p1136).

Dissimilar to the wolf spider, males of this species did not make an investment. "Nevertheless, males can also be choosy if the variability in female quality is high" (Sentenska and Pekar 2013 p1137).

1.3. APPENDIX 1A - BARRY ET AL (2008)

The foraging strategy hypothesis assumes that females who use SXC after copulation will have increased fecundity compared to non-SXC.

Barry et al (2008) studied the false garden mantid (Pseudomantis albofimbriata) in Australia. In a laboratory situation, where a virgin male and female were placed together, eight females were cannibalistic and nineteen not. The egg mass and female body condition were measured before and after copulation. There was a significant difference: "all females that consumed male conspecifics substantially improved their condition, whereas all non-cannibalistic females saw a decrease in body condition" (Barry et al 2008 p712). Fecundity was also improved by SXC.

In another experiment the researchers varied the availability of food prior to the copulation opportunity. Eight of nine females who have been starved cannibalised the males compared to zero of ten in the well-fed experimental condition.

In summary, "a female's body condition after trial was a significant predictor of her subsequent reproductive output, suggesting that females gain an immediate fecundity benefit as a direct result of male consumption. Pseudomantis albofimbriata males represent a relatively large proportion of a conspecific female's body mass, so it is not surprising that sexual cannibalism can boost the reproductive output of a female by up to 40%" (Barry et al 2008 p713).

1.4. APPENDIX 1B - SEA SLUG

Autotomy is "the voluntary shedding of a body part", and it is "generally followed by regeneration of shed terminal body parts, such as appendages or tails" (Mitch and Yusa 2021 pR233). It can be used as an extreme survival strategy against predators.

Mitch and Yusa (2021) reported an example of extreme autotomy in two species of sacoglossan sea slug that involved shedding the whole body. The reason for this ability is "unclear at present" as "adult sacoglossans generally have few predators due to their cryptic colouration and presence of toxic chemicals incorporated from their food" (Mitch and Yusa 2021 pR234). The researchers tried to imitate predator attacks in experiments, but this did not induce autotomy. Mitch and Yusa (2021) thus speculated that the function was the removal of internal parasites. All individuals observed in the laboratory to autotomise had a parasite (which occupied most of the slug's body and inhibited reproduction). After regeneration the slugs were parasite-free. "Parasitic autotomy" has been observed in earthworms (Mitch and Yusa 2021).

Alternative explanations include "to escape from being tangled in algae or to remove accumulated toxic chemicals" (Mitch and Yusa 2021 pR234).

1.5. REFERENCES

Aisenberg, A et al (2011) male sexual cannibalism in a sand-dwelling wolf spider with sex role reversal Biological Journal of the Linnean Society 103, 68-75

Barry, K.L et al (2008) Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity Behavioural Ecology 19, 710-715

Baruffaldi, L & Andrade, M.C.B (2021) Female control of a novel form of cannibalism during copulation in a South American widow spider Behavioural Processes 188, 104406

Elgar, M.A & Nash, D.R (1988) Sexual cannibalism in the garden spider Araneus diadematus Animal Behaviour 36, 1511-1517

Mitch, S & Yusa, Y (2021) Extreme autotomy and whole-body regeneration in photosynthetic sea slugs Current Biology 31, R233-R234

Sentenska, L & Pekar, S (2013) Mate with the young, kill the old: Reversed sexual cannibalism and male mate choice in the spider Micaria sociabilis (Araneae: Gnaphosidae) Behavioural Ecology and Sociobiology 67, 1131-1139

2. CULTURAL EVOLUTION AND LEARNING

2.1. CUMULATIVE CULTURAL EVOLUTION

"Collective knowledge" (or collective action or intelligence) is where "significantly more is achieved by the collective than is possible for any one individual alone" (Whiten et al 2021a p1). Terms like "the wisdom of the crowd", "consensus decision-making", and the "extended mind" have been used (Whiten et al 2021a) [1].

Whiten et al (2021a) asked some core questions about this phenomenon, including:

- How do collectives share knowledge beyond that accessible to individuals alone?

- Are the benefits of the collective over the individual temporary or more permanent?

- Do collectives create new behaviours beyond the individuals alone?

Large aggregates of animals (eg: bird flocks or insect swarms) are good examples of the collective phenomenon. "Key principles identified emphasise that much of collective animal behaviour is 'self-organised' [Camazine et al 2001], relying on relatively simple local interactions of individuals with their neighbours and with the environment, in the absence of any 'global' overseer or leader" (Whiten et al 2021a p2).

Research on non-human culture has a number of key limitations, including (Whiten et al 2021b):

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[1] Also called "swarm intelligence" ("improved cognitive performance that stems from distributed, self-organised decision-making, with decisions emerging from repeated local interactions between individuals") or "pool-of-competence effects" ("effects arising from group size and diversity, with larger groups being statistically more likely to include more experienced, motivated, persistent or bold individuals that are more likely to solve problems and from which others in the group can acquire information") (Webster et al 2017).

i) "One-to-one transmission" field studies that focus on one behaviour only. It is now accepted that, for example, "monkeys and apes sustain long-lived cultures defined by group-wide traditions spanning multiple domains of behaviour" (Whiten et al 2021b p2).

ii) "Social learning experiments" which compare solving a task after observing a model to a non-model control group. The experimental and control conditions are "not necessarily identical" (Whiten et al 2021b p2), for example.

"Later, 'two-action' designs improved on this approach by incorporating conditions in which each subject witnessed a model performing one of two (sometimes more) alternative acts on the same target objects. Where subjects adopt the particular model variant they witness, one can then examine whether and to what extent these variants spread and are sustained as alternative traditions at the group level" (Whiten et al 2021b p2).

Other more sophisticated experimental designs include "linear transmission chains" that show transmission of behaviours across generations, "open group diffusions" which introduce trained individuals into whole populations, and "replacement designs" "in which experienced individuals are removed from groups and naive individuals repeatedly introduced, testing the capacity of such collectives to sustain traditions through such simulated population turnovers" (Whiten et al 2021b p2).

The transmission and adaptation of information (as in culture) can be seen in a study with pigeons (Sasaki and Biro 2017). Two pigeons were tracked on several homing flights before one of the birds was replaced by a naive individual. The new pair were allowed to fly several homing flights before the more experienced bird was replaced by a naive individual. Now the pair was completely different to the original pair, but a more efficient homing flight had emerged. Whiten et al (2021a) summarised what this experiment demonstrated: "(i) the transmission, across pairings, of information underlying good flight paths generated up to that point; (ii) a capacity of consecutive pairs not only to share this information, but in interaction, improve it; and thence (iii) create cumulative cultural progress across the whole sequence of repeated replacement pairings" (p2).

This could be described as an example of Type I cumulative cultural evolution (CCE) (as opposed to Type

II) (Derex 2021) [2]. Type I "optimises exploitation of only a given set of phenomena... [whereas]... Type II is distinguished by recruiting additional and different natural phenomena, as in such examples as the bow and arrow superseding thrown spears in human history" (Whiten et al 2021a p8) (appendix 2A).

Mesoudi and Thornton (2018) outlined four "core criteria" of CCE:

i) Change in behaviour.

ii) Transmission through social learning.

iii) Improvement in performance.

iv) Sequential repetition of above criteria (Whiten et al 2021a).

Another example of Type I CCE comes from Wild et al (2021) (appendix 2B), while a possible example of Type II CCE in an experimental situation was performed by Vale et al (2017) (table 2.1) (Whiten et al 2021a).

- Each of six groups of chimpanzees were presented with a container of juice through a mesh fence and a variety of "tools" to access the juice. These included probes to dip into the juice and straws, but the most efficient was a folded tube ("long bendy tool"; LBT).

- Three groups of chimpanzees were allocated to the "seeded" condition where an experimenter showed one chimpanzee in each group how to use the LBT. The "unseeded" condition, involving the other three groups of chimpanzees had no model.

- After ten hours of exposure, the majority of chimpanzees in the seeded condition had used the LBT in some way way compared to very few chimpanzees in the unseeded condition.

- In the unseeded condition, however, four individuals learned by trial-and-error to use the LBT in an unusual way, and their behaviour spread through the group.

Table 2.1 - Details of Vale et al (2017).

"Experience pooling" was a term coined by Webster et

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[2] Examples of cultural traits in non-human animals have been found in recent years, and that "these animal cultures are not static, but can change over time in response to Darwinian-like processes such as drift and cultural selection" (Wild et al 2021 p1). But whether the change is the same as progressive refinement and complexity as seen in humans and in CCE is debated (Wild et al 2021).

al (2017) from their experimental work with sticklebacks. The researchers created a two-step task to reach hidden food within a mesh feeder box - stage 1: navigating a structured environment towards a light, and stage 2: swimming through a small hole. Some fishes were taught part of the task, but no individual had experience of both stages. Then four different types of shoals (of nine fish) were tested:

1. Only naive fish (no knowledge of stages 1 and 2).

2. Naive fish (majority - 6) and those taught stage 1 (3 fish).

3. Naive fish (majority - 6) and those taught stage 2 (3 fish).

4. Naive fish (one-third) and one-third taught stage 1 and one-third stage 2.

The latter shoal was most successful in terms of number of members reaching food and speed in doing so (Whiten et al 2021a).

Whiten and van de Waal (2018) described three main phases to social learning in the wild in primates: "first, a focus on the mother, second, on a progressively enlarging social network of other models, and third on new companions gained as adults disperse to join other groups. In phase 2, for example, young male primates may apprentice themselves to adult males whose diet is different to their mothers' and hence acquire the collective knowledge spanning the two sexes" (Whiten et al 2021b p7).

2.1.1. Dolphins

Ramos et al (2022) observed: "Bottlenose dolphins (Tursiops spp) display a remarkably diverse array of individual and co-operative foraging tactics across their global distribution that typically reflect local adaptations to habitat conditions and prey types" (p364). These specialist foraging methods include (Ramos et al 2022):

i) Strand feeding (eg: Sargeant et al 2005) - The catching of fish in very shallow water by the dolphins partially beaching themselves.

ii) "Kerplunking" - This behaviour observed in Western Australia "occurs over shallow offshore seagrass beds (1.5–2.5 m). Individuals lift their peduncle high into the air before bringing their flukes down at a steep angle with respect to the water surface, driving their flukes into the water (Connor et al 2000). The resultant cavitation produces a 3–4 m high vertical splash and accompanying pulsive sound that is thought to startle prey hiding in the seagrass" (Connor 2001 p329).

iii) Co-operation with fishermen (Pryor and Lindbergh 1990) - Humans and bottlenose dolphins appearing to work together to capture fish in Brazil.

iv) Foraging in and around trawl nets (Kovacs and Cox 2014) - Dolphins capturing prey disturbed by shrimp trawler nets off Georgia, USA.

v) Use of sponges or shells as tools (eg: Smolker et al 1997) - Using sponges or shells to protect the snout as dolphins trawl the sandy sea bottom for hidden prey.

vi) "Mud ring feeding" by common bottlenose dolphins in Florida Bay, USA (eg: Engleby and Powell 2019) - "This tactic involves a single 'ring-maker' dolphin (typically in a group) that swims rapidly in a circle near the seafloor along shallow inner-basin mud banks. Strong fluke kicks against the muddy substrate create a large circular mud plume or mud ring barrier used to encircle a fish school, commonly mullet (Mugil spp). Once the prey are encircled, individual dolphins wait with open mouths and lunge to catch airborne fish as they attempt to flee at the water's surface" (Ramos et al 2022 p364).

Ramos et al (2022) confirmed this latter behaviour in coastal bottlenose dolphins off Mexico and Belize using data from 2012 to 2019 collected in a variety of ways - boat-based photographs, aerial observations, and satellite imagery.

The tactic was used slightly differently here than to Florida Bay, but the principle of prey disorientation seemed common. For example, the species of prey was not known compared to mullet exclusively in Florida Bay. In the latter case, the fishes are caught as they try to leap away, but this was not so in Ramos et al's (2022) observations.

Ramos et al (2022) concluded that their study "supports the idea that habitat characteristics, and/or prey types and their behaviour, play a pivotal role in shaping the foraging tactics used by coastal dolphins. We have documented behavioural convergence between two geographically separate locations that share habitat characteristics, leading dolphins to develop similar strategies for prey capture" (p370).

2.2. INNOVATIVE LEARNING

Innovations by wild animals living in cities is an interesting area to study for behavioural flexibility and culture spread.

For example, sulphur-crested cockatoos (Cacatua galerita) opening lids of "wheelie bins" (plastic household waste bins on wheels) in Sydney and Wollongong, Australia (Klump et al 2021). Data were collected via an online "community science" survey (n = 1396 reports by 1322 respondents) in 2018 and 2019. Respondents were asked to describe when and where they saw the lid opening behaviour. Spatial analysis of the reports showed a spread from three to forty-four suburbs in Sydney, suggesting social learning.

The researchers video-recorded 160 successful lid opening sequences and analysed the stages of the behaviour - five: pry lid, open, hold, walk with lid, and flip lid fully open (Klump et al 2021).

Observations in one particular "hotspot" identified 114 individuals, of which nine cockatoos successfully opened bins while 27 were unsuccessful. The key characteristics of the former were male (90% of observations), and higher in the male dominance hierarchy.

2.3. TOOL USE

Tool use among non-human animals has been observed in a small, but growing, number of species. However, O'Hara et al (2021) warned, "not all tool use requires intelligence. When studying tool use, it is crucial to distinguish innovative (spontaneously acquired, learned individually, or spread socially) from specialised (inflexible, species-wide) tool behaviour" (p4512). Fragaszy and Mangalam (2018) presented a framework for defining tool use (or "tooling") as "a body-plus-object system that creates a biomechanical interface between a held object and the target" (O'Hara et al 2021 p4512). This approach also considers the evolution of the behaviours in the species.

Most of the interest is around non-human primate tool use, but among birds, there is evidence in parrots. O'Hara et al (2021) focused on one parrot species, the Goffin's cockatoo (Cacatua goffiniana) found on the Tanimbar Islands, Indonesia. "Like all parrots, they lack food caching or nest building ancestry. Nevertheless, they have a strong, playful urge to combine objects and are opportunistic extractive foragers, which are characteristics associated with tool innovations" (O'Hara et al 2021 p4513).

Auesperg et al (2016) reported sophisticated tool use by Goffins in the laboratory. But "it remains an open question whether these capacities are a product of being raised in an artificial captive environment" (O'Hara et al 2021 p4513). Hence the use of naturalistic observation data by O'Hara et al (2021).

From over 800 hours of observations, tool use and manufacture to extract seeds from a tropical fruit (Wawai mango) was reported by two Goffins (who were temporarily at a field aviary). Branch fragments were used to extract the seed matter. There was also evidence of three different tool "types" being used. However, thirteen other Goffins at the aviary did not show tool use in the same situations. "The limited occurrence of such a complex skill implies that it is not a species-wide trait but has been acquired in the natural environment" (O'Hara et al 2021 p4515).

APPENDIX 2A - TYPE I AND II CCE

Tool use exploits "natural phenomena". For example, stone tools exploit a harder substance to slice through softer materials, or a bow uses "elastic properties of materials such as wood to store elastic energy and convert it to kinetic energy" (Derex 2021 p1). The "ability to both expand the range of interdependent natural phenomena that we exploit and pass on the means of exploiting these phenomena to others is ultimately what underlies the open-ended dynamic that characterises human cumulative culture" (Derex 2021 p2).

Type I CCE is an "optimisation process" where the use of a natural phenomenon is exploited fully (eg: bows becoming better), but this "cannot lead to the emergence of new cultural traits and has only limited scope for pushing forward their efficiency" (Derex 2021 p2). However, Type II CCE is "more akin to an innovation process" and "bears the possibility of generating myriad cultural traits and continuous improvement" (Derex 2021 p2).

Chimpanzees have been observed to bite the tip of branches to produce very basic spears with which to hunt bushbabies (Pruetz and Bertolani 2007). Type I CCE could include improving the sharpness of the spear through more sophisticated biting procedures. "Yet, after some time, opportunities for improvement will start to dry up as individuals will move closer to a fixed optimum. Indeed, biting branches eventually causes fibres to become crushed and damp, which ultimately sets an upper limit to the perforating power of spears produced in this manner. No amount of biting, expertise in biting, faithfulness in biting skills transmission, or combination of biting methods would allow chimpanzees to get beyond this upper limit" (Derex 2021 p3).

Type II CCE might include the innovation of a sharp-edged stone to use in sharpening the spear tip. "The removal of initial constraints will pave the way for a new period of cultural optimisation by which sharpening procedures will be improved. After a while, opportunities for improvement will start to dry up again as solutions approach the new fixed optimum. The tip of very sharp spears, for instance, will be prone to failure, which will force individuals to balance perforating capabilities with robustness. At this point, new natural phenomena must be harnessed to push the efficiency of spears further" (Derex 2021 p3).

2.5. APPENDIX 2B - WILD ET AL (2021)

Wild et al (2021) studied great tits (Parsus major) in Wytham Woods, near Oxford. Previously (Aplin et al 2015), a sliding-door puzzle-box was introduced, which involved moving a small door to the left or right to gain access to food. Birds trained to move the door in one direction were introduced into sub-populations in the woods. The wild individuals learned to open the door in the direction of their "teacher". When the puzzle boxes were introduced the next year, it was found that the learning had been transmitted to the next generation. This was tried again the next year (Aplin et al 2017).

The research reported by Wild et al (2021) took place in the fourth year, and added a circular dial to the puzzle-box. There was now two steps to access the food (dial turning and door sliding). The researchers also varied the reward with one step (the sliding door) only leading to a low reward (sunflower seed), but performing both steps allowed access to a mealworm (high reward).

Two males each from four sub-populations in the woods were taught to turn the dial (clockwise or counter-clockwise). The sub-populations were subsequently observed to see if learning was transmitted, and then the next year the birds were observed. Learning to turn the dial would show the diffusion of the behaviour, but would previous knowledge (of the sliding door) be combined to solve the two steps?

Around one-fifth of birds learned to turn the dial, with a bias towards the direction of the "teacher". Overall, 6% of birds showed the two-step solution. The next year seventeen experienced and fourteen naive birds showed the two-step solution.

Wild et al (2021) summed up: "Similar to previous results, we found that simple foraging behaviours could spread and establish as new foraging traditions in wild great tits, giving further evidence for social learning and the spread of innovation in this species. When provided with the opportunity to chain these traditions together in a foraging task that gave progressive rewards, a proportion of the population were also able to do so. However, birds were generally not able to learn the complex behaviour ex-nihilo, and its acquisition instead depended on social learning of the individual components before individual reconstruction of the full complex behaviour" (p9).

2.6. REFERENCES

Aplin, L.M et al (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds Nature 518, 538-541

Aplin, L.M et al (2017) Conformity does not perpetuate sub-optimal trends in a wild population of songbirds PNAS 114, 7830-7837

Auersperg, A.M.I et al (2016) Goffin's cockatoos make the same tool from different materials Biology Letters 12, 2-5

Camazine, S et al (2001) Self-Organisation in Biological Systems Princeton, NJ: Princeton University Press

Connor, R.C (2001) Individual foraging specialisations in marine mammals: Culture and ecology Behavioural and Brain Sciences 24, 2, 329-330

Connor, R.C et al (2000) "Kerplunking": Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins Marine Mammal Science 16, 3, 646-653

Derex, M (2021) Human cumulative culture and the exploitation of natural phenomena Philosophical Transactions of the Royal Society B 377, 20200311

Engleby, L.K & Powell, J.R (2019) Detailed observations and mechanisms of mud ring feeding by common bottlenose dolphins (Tursiops truncatus truncatus) in Florida Bay, Florida, USA Marine Mammal Science 35, 3, 1162-1172

Fragaszy, D.M & Mangalam, M (2018) Tooling Advances in the Study of Behaviour 50, 177-241

Kovacs, C & Cox, T (2014) Quantification of interactions between common bottlenose dolphins (Tursiops truncatus) and a commercial shrimp trawler near Savannah, Georgia Aquatic Mammals 40, 1, 81-94

Klump, B.C et al (2021) Innovation and geographic spread of a complex foraging culture in an urban parrot Science 373, 456-460

Mesoudi, A & Thornton, A (2018) What is cumulative cultural evolution? Proceedings of the Royal Society B 285, 20180712

O'Hara, M et al (2021) Wild Goffin's cockatoos flexibly manufacture and use tool sets Current Biology 31, 4512-4520

Pruetz, J.D & Bertolani, P (2007) Savanna chimpanzees, Pan troglodytes verus, hunt with tools Current Biology 17, 412-417

Pryor, K & Lindbergh, J (1990) A dolphin-human fishing co-operative in Brazil Marine Mammal Science 6, 1, 77-82

Ramos, E.A et al (2022) Lords of the rings: Mud ring feeding by bottlenose dolphins in a Caribbean estuary revealed from sea, air, and space Marine Mammal Science 38, 364-373

Sargeant, B.L et al (2005) Specialisation and development of beach hunting, a rare foraging behaviour by wild bottlenose dolphins (Tursiops sp) Canadian Journal of Zoology 83, 11, 1400-1410

Sasaki, T & Biro, D (2017) Cumulative culture can emerge from collective intelligence in animal groups Nature Communications 8, 15049

Smolker, R et al (1997) Sponge carrying by dolphins (Delphinidae, Tursiops sp): A foraging specialisation involving tool use? Ethology 103, 6, 454-465

Vale, G.L et al (2017) Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture Evolution and Human Behaviour 38, 635-644

Webster, M.M et al (2017) Fish pool their experience to solve problems collectively Nature Ecology and Evolution 1, 0315

Whiten, A & van de Waal, E (2018) The pervasive role of social learning in primate lifetime development Behavioural Ecology and Sociobiology 72, article 80

Whiten, A et al (2021a) The emergence of collective knowledge and cumulative culture in animals, humans and machines _Philosophical Transactions of the Royal Society B_ 377, 20200306

Whiten, A et al (2021b) Collective knowledge and the dynamics of culture in chimpanzees _Philosophical Transactions of the Royal Society B_ 377, 20200321

Wild, S et al (2021) Complex foraging behaviours in wild birds emerge from social learning and recombination of components _Philosophical Transactions of the Royal Society B_ 377, 20200307

3. COPROPHAGY

3.1. INTRODUCTION

"The term 'coprophagy' literally means faeces-eating, where 'faeces' could conceivably be of various kinds: faeces of other species or of the conspecifics; those of other individuals (allocoprophagy) or its own (autocoprophagy); those once deposited or taken directly from the anus" (Hirakawa 2001 p61).

In terms of reasons for the behaviour, studies have found that coprophagy provides vitamins and nutrients to young pigs and horses, for instance, and bacteria to help in digestion of plant materials in gorillas. The softening of hard seeds is also a reason for coprophagy (Fish et al 2007). While the rufous hornero (or red ovenbird) (Furnarius rufus) is known to build its nest with fresh faeces (Leuchtenberger et al 2012).

3.2. PIKA

Endothermic animals internally regulate their body temperatures irrelevant of the environment, but as it gets colder more energy is required to do this, "particularly in small animals that have a less favourable surface-to-volume ratio. Since cold conditions during the arctic and temperate winter often also coincide with reductions in food supply, this creates a problem for small endothermic animals that do not migrate or hibernate" (Speakman et al 2021 p1).

One strategy used by red squirrels, for example, is to reduce physical activity, remain in well-insulated nests surviving on hoarded food. "In contrast, hares do not store food, do not exploit nests or burrows, and remain exposed to the winter environment. They survive primarily by adopting physiological mechanisms that increase thermogenesis and sustain high invariant body temperatures" (Speakman et al 2021 p2).

Speakman et al (2021) studied the strategy of the plateau pika (Ochotona curzoniae) (figure 3.1) living on the Qinghai-Tibetan Plateau in Central Asia (figure 3.2). It is a high-altitude desert with low precipitation and vegetation, low oxygen partial pressure, and with temperatures of -30 °C in the winter. Pikas at two sites were studied between 2007 and 2020.

(Source: Kunsang)

Figure 3.1 - Plateau pika.

Daily energy expenditure (DEE) was measured by the doubly labelled water (DLW) method, which involves the injection of certain isotopes into the body and their breakdown in body fluids like urine or blood can be used to calculate metabolic rate and subsequently DEE. DEE was calculated to be significantly lower in the winter than the summer (adult mean: 169.2 vs 280.3 kJ/d (kilojoules per day)). In the face of cold temperatures, DEE was achieving by reducing physical activity, and body temperature.

One interesting finding was that pika numbers were higher where domestic yak numbers were higher, though they are "supposed direct competitors for food" (Speakman et al 2021 p1). It was directly observed that pikas ate

(Source: Chermundy)

Figure 3.2 - Qinghai-Tibetan Plateau area.

yak faeces to supplement their food intake in winter, and this explained the abundance of both species together. This inter-species coprophagy (table 3.1) was confirmed by identification of yak DNA in the pika stomach contents. Eating faeces reduced DEE in foraging [3].

Speakman et al (2021) outlined other benefits to this behaviour: "First, having been processed by the yak digestive system, yak faeces may have lower levels of plant toxicants. American pika put plants containing high levels of phenolics into their haypiles and do not consume them until the levels have declined. Second, because the food is partially digested by the yak, it may be more easily digested by the pika. Animal excreta

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[3] Autocoprophagy has been reported in pika species (Horakawa 2001).

generally are suggested to be rich in amino acids, vitamins, and minerals. Coprophagy in chimpanzees (Pan troglodytes) has been speculated to improve digestion of Dialium seeds (Dialium spp. [Caesalpiniaceae])" (p9).

Furthermore, "yak faeces may provide a source of water, given the available vegetation is so dry, and any surface water is frozen. Feeding on a highly digestible and readily available food source like yak faeces may reduce the time they need to spend on the surface, and such reduced surface activity may lead to benefits in reduced exposure to aerial predators, such as, peregrine falcon (Falco peregrinus) and buzzards (Buteo refectus) that are routinely seen at these sites, along with terrestrial predators like the Tibetan fox (Vulpes ferrilata), a specialist pika predator, none of which can access the pikas when they are in their burrows" (Speakman et al 2021 p9). However, this is a risk of ingesting gut parasites with eating faeces.

Eater	Provider	Study
Sika deer	Macaque	Nishikawa & Mochida 2010
Reindeer	Barnacle goose	van der Wal & Loonen 1998
Wilson's storm petrel	Northern right whale	Kraus & Stone 1995
Giant petrel	Weddell seal	Cora et al 2020
Ring tailed lemur	Human, cattle, dog	Fish et al 2007
Cave dwelling salamander	Bat	Fenolio et al 2006
Various	Giant otter	Leuchtenberger et al 2012

(Source: Speakman et al 2021 supplementary materials)

Table 3.1 - Examples of inter-species coprophagy (appendix 3A).

3.3. CORAL REEF FISHES

Parrotfishes and surgeonfishes are "nominally herbivores" grazing on turf algae and the epilithic algal matrix (EAM) in the coral reef ecosystem. There have been limited reports of coprophagy by these fishes to supplement their herbivorous diet. "Coral reefs are typically nutrient-limited ecosystems. Algae are generally considered to be of low-nutritional quality in the diets of herbivorous fishes... as they are relatively low in protein and contain carbohydrates that are difficult to digest for fishes with a limited capacity for hindgut fermentation, such as parrotfishes" (Rempel et al 2022 p3).

Rempel et al (2022) studied the consumption of Brown Chromis faeces by nine parrotfish and three surgeonfish species on the coral reef off the Southern Caribbean island of Bonaire in 2019. The researchers observed 135 faecal pellets, of which 85% were consumed, 4% were tasted but not ingested, less than 1% inspected only, and the remainder were uninspected. So, there were 114 pellets consumed, and over 90% of this was by parrotfishes or surgeonfishes. Some species of these fishes consumed more than others - all three species of surgeonfish and six of the nine parrotfish species.

Analysis of faecal pellets established that the nutritional value was greater than the EAM. The Brown Chromis is a planktivore, so there will be macronutrients (eg: protein) and micronutrients (eg: trace elements) in the faeces different to the EAM. Rempel et al (2022) concluded that faecal pellets were an "important but overlooked component" (p9) of the diet of parrotfishes and surgeonfishes.

The researchers were not sure if the observed behaviour was unique to Bonaire. Coprophagy by similar fish species had been observed in the Indo-Pacific coral reef (Robertson 1982), and Brazil (Sazima et al 2003).

3.4. AUTOCOPROPHAGY

Autocoprophagy directly from the anus has also been called "refection" or "reingestion", and it is "not merely a recycling of undigested materials, but has a specific digestive function" (Hirakawa 2001 p61). It is a behaviour of small- to medium-sized herbivorous mammals.

Caecotrophy is the reingestion of soft faeces, which are rich in vitamins and microbial proteins, by animals that produce two types of faeces (hard and soft) (eg: domestic rabbits) (Hirakawa 2001).

Caecotrophy seems to be "an indispensable part of the digestion process" (Hirakawa 2001 p62) as rabbits prevented from reingestion develop malnutrition. There is a rhythm to the behaviour that has been observed. For example: "In the Japanese and the Mountain Hare, hard faeces are ingested for the first hour of resting in the morning, then soft faeces until the early afternoon, and then again hard faeces until dusk when hares leave the form to start night-time activity... While feeding at night, the Japanese Hare excreted hard faeces, all of which were discarded; but if food is not available, hard faeces were reingested instead" (Hirakawa 2001 p65).

The reingestion of hard faeces can be described as "pseudo-rumination", as it is the "equivalent to rumination in pre-gastric fermenters [eg: beef cattle] , in the sense that it is practised during the resting phase and that poorly digestible large particles are remasticated and ground into fine particles" (Hirakawa 2001 p69).

Reingestion is most common in leporid herbivores (ie: rabbits and hares), but there are reports in many rodent species, and some marsupials (Hirakawa 2001).

Hirakawa (2001), in categorising the styles of reingestion, distinguished six characteristics:

i) Frequency of reingestion.

ii) Timing of reingestion in the daily feeding cycle (eg: overlap with feeding).

iii) Faeces examination behaviour (present or absent).

iv) Digestive processes involved (eg: separate processes to produce hard and soft faeces).

v) Differentiation of faeces (all of faeces or only selected pellets).

vi) Mastication (present or absent).

"Coarse plant material, like grasses and leaves, is generally poor in nutrients and contains a lot of barely digestible cellulose and hemicellulose. Herbivorous mammals digest these with a help of microbial fermentation in a specifically developed chamber. Ruminants like deer and cows, colobine monkeys, hippopotamuses and kangaroos have a fermentation chamber developed from the oesophagus (pre-gastric fermenter); horses, pigs and howler monkeys have it at the colon (colonic fermenter); and rodents and leporids at the caecum (caecal fermenter)" (Hirakawa 2001 p75).

In terms of explaining reingestion in small- and medium-sized herbivores, Hirakawa (2001) proposed that poorly digestible large particles are excreted quickly to maintain an efficient digestive system. So, the faeces can still have nutritional value.

The evolution of hard and soft faeces helped the animals know which type has the more nutritional value. It also allows them to live on low-quality food in environments where they are exposed to strong predation pressure (Hirakawa 2001).

3.5. APPENDIX 3A - VARIOUS STUDIES

van der Wal and Loonen (1998)

Barnacle geese (Branta leucopsis) on Spitsbergen consume grasses and mosses, which are the diet of Svalbard reindeer (Rangifer tarandus platyrhynchus). The digestive tract of the geese is swift and large amounts of cellulose is undigested in their faeces. Reindeers can digest cellulose.

van der Wal and Loonen (1998) performed two small-scale experiments in the summer of 1993. Fresh goose droppings were placed in an area which could be observed in the first experiment. While in the second experiment, droppings containing grass or moss were placed in different areas.

In ten of the fourteen trials of the first experiment, the majority of droppings were eaten. While in four trials of the second experiment, in all cases droppings containing grass were eaten, but not the droppings containing moss.

Chemical elements in the droppings can explain the behaviour. "Positive selection of potassium or avoidance of high concentrations of sodium and magnesium could result in a preference for grass droppings or grasses" (van der Wal and Loonen 1998 p1120).

Also droppings are a food source when grasses are not available.

Nishikawa and Mochida (2010)

On Yakushima Island, Japan, during the day Japanese sika deer (Cervus nippon yakushimae) forage on food that drops from trees containing Japanese macaques (Macaca fuscata yakui). This is known as "gleaning" (Nishikawa and Mochida 2010).

During night observations in 2009, Nishikawa and Mochida (2010) saw deer feeding on macaques' faeces. Both this behaviour and gleaning were believed to be seasonal, particularly in the post-birth season when females are in need of certain nutrients for their milk production. Analysis of the composition of the faeces was not made.

Cora et al (2020)

At Harvey Point, Nelson Island (Maritime Antarctic Peninsula), southern giant petrels (Macronectes giganteus) feed on carcasses, placenta, faeces, and regurgitations of Weddell seals (Leptonychotes weddellii). Twenty birds were tracked with GPS and observed over two months in 2019-20 by Cora et al (2020).

Both male and female southern giant petrels spend long periods incubating their egg and so they have decreased body resources. Birds were observed to visit the seal haul-out sites after nest-sitting and before going on long foraging trips out at sea (eg: 5-15 days). Cora et al (2020) concluded that "after a long period of fasting, southern giant petrels ingest seal faeces as a way to gain a quick intake of energy before starting a long foraging trip in search of more energetic food" (p2113). The petrels showed "resource defence behaviour patterns" (Cora et al 2020 p2113) over the faeces (eg: disputing access of others).

But the faeces is poor quality in terms of energy provision because when the chick had hatched, the petrels foraged at sea for shorter periods, and with shorter periods of fasting. They did not feed their chick with the faeces.

Fish et al (2007)

Fish et al (2007) reported the unusual behaviour of ring-tailed lemurs (Lemur cattra) consuming faecal matter of three other species (humans, cattle, and feral dogs). The observations of human faeces consumption took place at the researchers' camp in Madagascar with an easily accessible open latrine. The lemurs also fed on discarded human food.

The researchers noted that older lemurs were consuming human faeces. They suggested that such individuals "and/or dentally impaired ring-tailed lemurs may consume the faeces of other animals because it allows them access to nutrients that they are unable to obtain from harder food items such as tamarind fruit, which is an important dry season food for lemurs at this site" (Fish et al 2007 p716).

Fish et al (2007) commented on the risks of coprophagy: "By consuming faeces from other animals, ring-tailed lemurs may be exposing themselves to human, cow, and dog parasites... Because lemurs select dry faeces, they are potentially limiting their exposure to some human parasites that are not able to survive for extended periods of time in faeces. However, lemurs may come into contact with fresh faeces while foraging for dried human, dog, and zebu [humped cattle] faeces" (p717).

Leuchtenberger et al (2012)

Leuchtenberger et al (2012) observed with camera traps 21 communal latrines of six groups of giant otters (Pteronura brasiliensis) in the Pantanal of Brazil in 2010-11. This produced 584 photographs showing 29 vertebrate species visiting the latrines, and nine definitely eating faeces (eg: crab-eating fox; ocelot; chaco chachalaca).

So, the latrines provided food, micro-organisms to aid digestion of plant materials, and calcium in the fish bones. Leuchtenberger et al (2012) commented: "Some carnivores, as well as giant otters, consume their prey rapidly and portions of soft tissues can remain within the faeces, which may represent an important source of protein for some species mainly during periods of food scarcity... In our study, some species were seen eating from latrines only during the high-water season, when food availability is generally lower in the Pantanal" (p85).

3.6. REFERENCES

Cora, D.H et al (2020) Coprophagic behaviour of southern giant petrels (Macronectes giganteus) during breeding period Polar Biology 43, 12, 2111-2116

Fenolio, D.B et al (2006) Coprophagy in a cave-adapted salamander, the importance of bat guano examined through nutritional and stable isotope analyses Proceedings of the Royal Society B 272, 439-443

Fish, K.D et al (2007) Coprophagy by wild ring-tailed lemurs (Lemur catta) in human disturbed locations adjacent to the Beza Mahafaly special reserve, Madagascar American Journal of Primatology 69, 713-718

Hirakawa, H (2001) Coprophagy in leporids and other mammalian herbivores Mammal Review 31, 61-80

Kraus, S.D & Stone, G.S (1995) Coprophagy by Wilson’s storm petrels Oceanites oceanicus, on Northern right whale, Eubalaena glacialis, faeces Canadian Field Naturalist 109, 443-444

Leuchtenberger, C et al (2012) To each his own taste: Latrines of the giant otter as a food source for vertebrates in Southern Pantanal, Brazil Studies on Neotropical Fauna and Environment 47, 2, 81-85

Nishikawa, M & Mochida, K (2010) Coprophagy-related inter-specific nocturnal interactions between Japanese macaques (Macaca fuscata yakui) and sika deer (Cervus nippon yakushimae) Primates 51, 95-99

Rempel, H.S et al (2022) Faeces consumption by nominally herbivorous fishes in the Caribbean: An underappreciated source of nutrients? Coral Reefs (https://link.springer.com/article/10.1007/s00338-022-02228-9)

Robertson, D (1982) Fish faeces as fish food on a Pacific coral reef Marine Ecology Progress Series 7, 3, 253-265

Sazima, I et al (2003) The cetacean offal connection: Faeces and vomits of spinner dolphins as a food source for reef fishes Bulletin of Marine Science 72, 1, 151-160

Speakman, J.R et al (2021) Surviving winter on the Qinghai-Tibetan Plateau: Pikas suppress energy demands and exploit yak faeces to survive winter PNAS 118, 30, e2100707118

van der Wal, R & Loonen, M.J.J.E (1998) Goose droppings as food for reindeer Canadian Journal of Zoology 76, 1117-1122

4. MATING SYSTEMS AND SEXUAL SELECTION

4.1. SEXUAL SELECTION

Charles Darwin's original conception of evolution by sexual selection was that males compete for females, and females choose. "Darwin [1871] argued that this sex difference is virtually ubiquitous, claiming that 'with almost all animals, in which the sexes are separate, there is a constantly recurrent struggle between the males for the possession of the females' and that 'the female [...], with the rarest exception, is less eager than the male [...] she is coy and may often be seen endeavouring for a long time to escape from the male'" (Fromonteil et al 2021 p3).

Fromonteil et al (2021) criticised the dominance of this view even today, particularly as evidence shows that females compete for mates in the face of male choice. This is seen in "so-called sex-role reversal species" (eg: seahorses). In this case, "fertilisation takes place inside the brood pouch of the male, which provides all parental care. As a consequence, males become a limiting resource for which females compete, which eventually leads to selection for ornaments favoured by male pre- and even post-copulatory mate choice" (Fromonteil et al 2021 p4).

However, sexual selection in females "might actually be an omnipresent phenomenon in animals but operating less intensely and more subtly compared to males, which can make it more difficult to detect" (Fromonteil et al 2021 p5). Fromonteil et al (2021) performed a meta-analysis of 72 species to investigate this idea.

Overall, it was found that "females - just as widely assumed for males - typically benefit from having more than one mating partner... As a consequence, selection is also expected to favour the evolution of female traits that promote the acquisition of mating partners" (Fromonteil et al 2021 p13).

4.2. CALIFORNIA MOUSE

Monogamy is "classically defined as co-habitation, reproduction and pair-bonding with an opposite-sex mate" (Valentino et al 2021 p1).

Valentino et al (2021) explained that "the stable presence of a mate in strictly monogamous species confers the benefits of resource consolidation and guarding especially during periods of gestation and lactation... and co-parenting, which is promoted by males seeking paternity assurance while females seek paternal care security" (pp1-2).

DNA fingerprinting in recent years has shown that "100% fidelity is rare, however, even among strictly monogamous species" (Valentino et al 2021 p2).

In the monogamous California mouse (Peromyscus californicus), pair bonds are "thought to be maintained by males who mate guard, or aggressively isolate mates from rival males to prevent EPCs [extra-pair copulations]... as high levels of EPCs are observed when males leave the nest" (Valentino et al 2021 p2).

Valentino et al (2021) investigated re-pairing (RP) of mates among laboratory-reared California mice when a mate had died, or no litters had been produced in six months of pairing. Data were available on 584 breeding pairs at the university breeding colony (2015-2018). RPing involved the experienced individual being placed with an inexperienced individual. Birth latency (BL) (ie: number of days between pairing and birth of first successful litter) was the outcome measure.

Overall, 85% of RPs successfully birthed a litter (which is similar to original pairs - 89%). This suggested that "a monogamous species can and will remain reproductively active after losing a mate" (Valentino et al 2021 p3).

The mean BL in originally paired animals was 50 days compared to 60 days for RP. This was not statistically significant. But the BL was significantly longer when the RP animal was female than when male (mean 66 vs 56 days).

Valentino et al (2021) argued that "females may become 'choosier' when RPed because of reproductive costs associated with partner loss. In the California mouse, up to a 35 % reduction in offspring survival has been observed when fathers are removed" (p3).

All breeding pairs and RPing was forced by the researchers. In the wild, individuals would choose their own partners.

4.3. MONGOOSE AND CO-OPERATIVE BREEDING

Rawls (1971) argued that "impartiality or ignorance on the part of decision-makers promotes co-operation and fairness in human societies has a long pedigree in philosophy and economics. Individuals that are blind to their own gains are predicted to allocate resources for the good of the group rather than themselves, typically reducing inequality" (Marshall et al 2021 p2). Is there an analogy in non-human societies?

A "Mendelian veil of ignorance" was proposed by Okasha (2012), where, in insect societies, for example, "uncertainty over relatedness promotes co-operative behaviour: workers co-operate to raise the offspring of other workers when relatedness to offspring is uncertain, but kill such offspring when they can discriminate worker-laid vs queen-laid eggs" (Marshall et al 2021 p2).

Marshall et al (2021) studied banded mongooses (Mungos mungo) (figure 4.1) where there is co-operative

(Source: Daderot; in public domain)

Figure 4.1 - Captive banded mongooses.

breeding, and many females give birth on the same morning in a shared underground den. This "extreme birth synchrony" creates a "veil of ignorance" about parentage, and encourages all females to suckle and care for all pups.

Using a population of wild mongooses in Uganda, the researchers gave extra food to half of the pregnant females ("fed condition") as opposed to the normally fed controls ("non-fed condition"). This produced variations in offspring birth weight (ie: heavier in the fed condition). Would the mothers reduce or amplify these inequalities in the communal litter?

In total there were 101 fed and 97 unfed mothers. It was found that "fed mothers invested in needier offspring to whom they were unrelated, rather than in their own young" (Marshall et al 2021 p4). In other words, inequalities in the weight of the pups was reduced. Non-fed mothers showed no preference towards pups. This finding is the opposite to predictions that favour kin. But it fits a "veil of ignorance" model where mothers have evolved to invest in need because it is usually not possible to know who is kin and who is not.

Marshall et al (2021) explained that "mothers invest post-natally to minimise the risk that their own offspring will face a disadvantage. Our findings show that uncertainty about kinship in a non-human species can lead to a redistribution of resources to reduce inequality, consistent with the proposed role of the veil of ignorance in the evolution of human fairness norms" (p5).

4.4. PARASITOID WASP

"In most sexually reproducing organisms, male reproductive success is limited by the number of fertile females it can mate. In contrast, female reproductive success is mainly limited by the number of eggs produced... This difference necessitates distinct reproductive strategies for both... For a male, the ideal reproductive strategy involves rapid sexual maturation and access to many fertile females" (Prazapat et al 2022 p2).

Male mate-finding strategies are thus important. Parasitoid wasps have been well studied here. The ability to detect chemica cues from the female, even before leaving the host is one way. In another species, the male emerges from the host first, waits for emerging females and mates (Prazapat et al 2022).

Prazapat et al (2022) investigated the cues used by males to detect females in the fly host in four species of Nasonia parasitoid wasps. Firstly, the researchers established that males could detect parasitised hosts by offering a choice between a two-day old parasitised host and an unparasitised host. The males spent significantly more time on the former.

Males were given the choice next between two parasitised hosts - one containing all males and other males and females. Only one species (Nasonia vitripennis; figure 4.2) showed a significant preference for the latter, while the other species showed no preference.

Focusing now on the type of cues used by the males of the Nasonia vitripennis, the following conclusions were drawn:

a) Auditory cues - No preference between hosts containing live or dead wasps.

b) Visual cues - The host pupa's outer casing (puparium) changes colour, but this did not influence the males.

c) Olfactory cues - The males did respond to cues emanating from the wasps in the host. The researchers felt that the olfactory cues in particular were cuticular hydrocarbons of females.

(Source: M.E Clark; public domain)

Figure 4.2 - Nasonia vitripennis.

4.5. FRUIT FLIES

Male fruit flies perform an elaborate courtship ritual, which involves following a mate and singing to her to entice her to copulate (Sten et al 2021).

Sten et al (2021) investigated the visual trigger for this behaviour with a "virtual" female on a screen. The tethered male was initially indifferent to the visual stimulus until particular neurons (P1) fired. Pheromones play a role, but are "not essential to arouse a male" (Sten et al 2021 p550).

"In the wild, Drosophila meet and mate on fermenting fruits, where diverse species frequently congregate. Consequently, a male must not only be persistent in his courtship to entice choosy females to copulate, but also remain sensitive to sensory feedback to prevent continued pursuit of inappropriate or unreceptive mates" (Sten et al 2021 p553). The P1 neuron activity functions "like a rheostat" (p553) to balance the need for persistence and flexibility in the courtship ritual. This appears similar to "an innate releasing mechanism from classic ethology" (Sten et al p553).

An enhanced sensitivity to moving targets is important. "Indeed, transient activation of P1 neurons drives persistent courtship displays even towards inanimate objects, suggesting that these neurons gate an enduring state of sexual arousal" (Sten et al 2021 p549).

4.6. DIVORCE AND BIRDS

Pair bonding (social monogamy) is estimated in at least 80% of species of birds (Wilson et al 2022). "Selecting a good mate is particularly important for species with long-term partnerships, since an individual's lifetime fitness will depend, in large part, on contributions made by a single partner, including genetic contributions that influence heritable qualities of offspring (indirect fitness effects) and contributions of non-genetic resources that influence fecundity and offspring survival (direct fitness effects...)" (Wilson et al 2022 p51).

Divorce may occur within or between breeding seasons. "Trading up" is one reason (ie: finding a partner of higher quality) or finding a more compatible partner is another. "The frequency of divorce in pair-bonding species should vary not only with the fitness costs of separating from sub-optimal mates, but also with the opportunities for finding alternatives of higher quality or compatibility" (Wilson et al 2022 p51).

Wilson et al (2022) investigated divorce in an experiment with zebra finches (Taeniopygia guttata) in captivity. Two variables related to males were tested -

quality (based on two secondary sexual traits - beak colour and cheek patch size), and bonding behaviours. It was predicted that males lower in these would be vulnerable to divorce.

Twelve flocks of twenty individuals (ten male and ten female) were created, and the birds were allowed to pair. New flocks were subsequently created with some paired birds, some separated pairs, and "bachelor" birds. This gave females the opportunity for divorce as new males were available.

Male beak colour or cheek patch size were not associated with divorce, nor bonding behaviours. Wilson et al (2022) were unsure about these findings. The two secondary sexual traits are known to influence mate choice by females. While certain bonding behaviours (eg: nest searching; high contact affiliative behaviours like allopreening) predicted divorce (ie: the opposite to expected). This may have been a product of the behaviour sampling technique used by the researchers. Scan sampling of the flock occurred for sixty minutes once or twice a day for five days by trained observers. However, the researchers preferred another explanation - "we suggest that prolonged displays of high-contact affiliative behaviours may be indicative of a pair failing to progress to the next phase of their shared reproductive effort, especially to settling on a nest site and/or to the onset of joint incubation that may result from conflict over nest site selection. Consistent with this logic, we observed that pairs that eventually divorced attended a greater number of nest sites than pairs that stayed together. This suggests the possibility that lack of agreement about nest site suitability during pair formation may be an early impetus to divorce" (Wilson et al 2022 p57).

Divorce was observed to be related to the presence of "bachelor" birds, and the fluid composition of the re-created flocks. This fits with an "opportunist" explanation for divorce.

There is the possibility that initial mate choice is based on attractiveness, say, but if this does not mean compatibility (eg: in nest site selection), then compatibility is more important in re-mating choice. This is supported by a study on barn owls (Dreiss and Roulin 2014), "where divorcing males re-paired with less ornamental, but more compatible, females" (Wilson et al 2022 p58).

Divorce resulted in a short-term reproductive cost. "Among birds that re-mated and those that did not, there was no difference in the number of eggs laid, but stable pairs produced more hatchlings and more fledglings compared to birds that re-mated" (Wilson et al 2022 p58). However, long-term gains of a compatible partner compensates.

Fluid social environments with opportunities for new partners will favour divorce and re-mating (Wilson et al 2022).

4.6.1. Albatross

Many species that are monogamous face the problem that because of "intra-sexual competition, the choice of mate is seldom unconstrained and many individuals in the population have to settle with a sub-optimal partnership" (Ventura et al 2021 p1). So, divorce is a possible solution (ie: not to remate in the following breeding season). This is described as the "win-stay, lose-switch" information gathering process (Ventura et al 2021). "For instance, in long-lived seabirds, the benefits resulting from breeding with the same partner (improved experience and co-ordination between the pair members owing to mate familiarity) and the high mate survival probability (which limits the costs of waiting in vain for the reunion with the old partner), as well as the costs involved in attracting and pairing with a new mate, result in low divorce rates" (Ventura et al 2021 p2).

Environmental conditions, however, may be an underlying factor behind divorce. The "habitat-mediated" hypothesis, for example, suggests that "divorce is more common in unstable and lower quality environments" (Ventura et al 2021 p2). Key is reproductive success in previous years. An alternative hypothesis is that "rather than being driven by the reproductive outcome per se, the decision of retaining or changing mate might be informed by the reproductive outcome relative to the environmental conditions experienced in a given year. Thus, environmental variability may affect the reliability of the 'win-stay, lose-switch' information gathered in previous years, potentially leading to a discounting of the importance of reproductive failures in bad years" (Ventura et al 2021 p2).

Ventura et al (2021) tested these hypotheses with long-term data on the black-browed albatross (Thalassarche melanophris) (figure 4.3) on New Island in the Falklands Islands (figure 4.4). Data collection began in 2003.

(Source: Francois Guerraz)

Figure 4.3 - Black-browed albatross at a nesting colony.

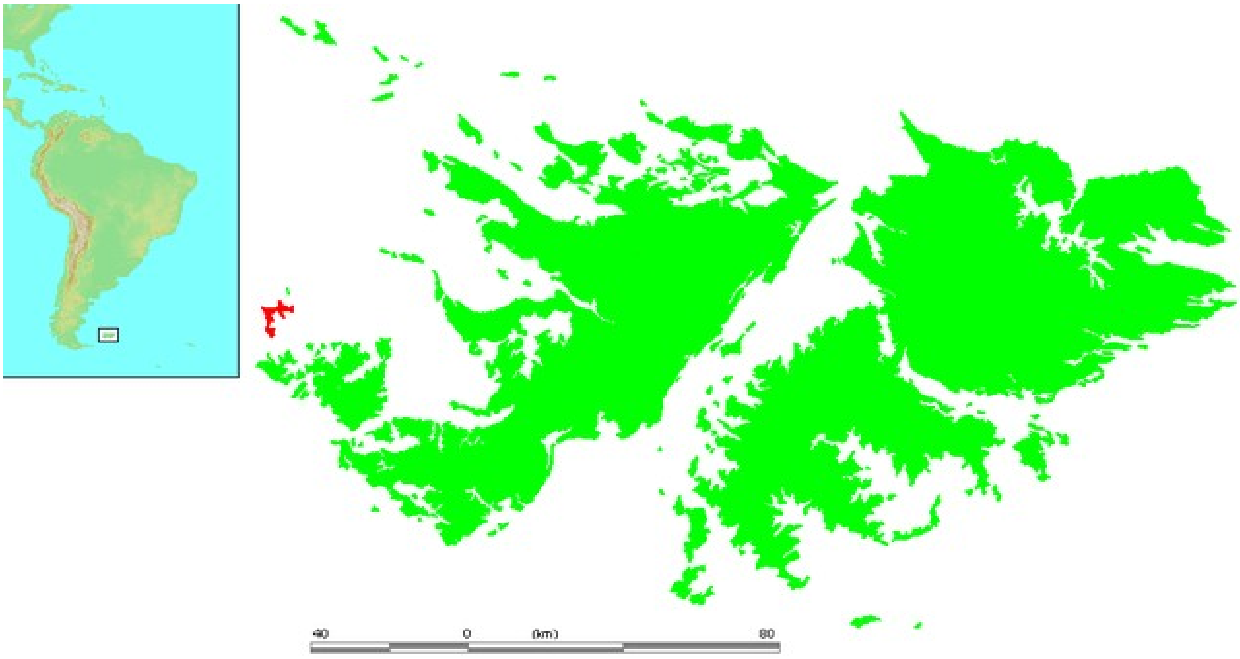
As well as details on the individual birds, there were environmental data, which included "sea surface temperature anomalies" (SSTA) and wind intensity (WIND). It was expected that SSTA would positively correlate with divorce and WIND negatively.

Divorce was defined as at least one member of the breeding pair re-pairing with a different mate in the following breeding season (while the prior partner is still alive).

The average divorce rate was calculated at 3.7% between 2004 and 2019. The divorce rate increased as SSTA increased.

Reproductive failure was key. Females whose eggs did not hatch in a breeding season were five times more likely to divorce than successful breeders. Female breeding success improved marginally after divorce, but males showed no difference.

In summary, breeding failure triggers divorce, which is beneficial for females (ie: "divorce is an adaptive strategy driven by the 'win-stay, lose-switch'



(Source: M.Minderhoud; public domain)

Figure 4.4 - Position of New Island and the Falkland Islands.

information gathering process"; Ventura et al 2021 p5). But the environmental conditions also impacted divorce (irrelevant of previous breeding success), which supported the "habitat-mediated" hypothesis. Poor environmental conditions, for instance, may mean that individuals are in a poor physiological state or there are asynchronous arrivals of the pair members at the breeding ground. Also, "hard environmental conditions and food shortage are associated with higher levels of circulating stress hormone corticosterone. Thus, after a difficult resource-poor breeding season, the greater effort and higher breeding investment can lead stressed females to disrupt the bond with their previous mate and look for a new one, even if previously successful" (Ventura et al 2021 p8).

Ventura et al (2021) ended that "in light of the dramatic extent of the current climatic changes, the environmentally driven disruptions of the breeding processes of socially monogamous populations might represent an overlooked consequence of global change, with repercussions on demography and population dynamics" (p8).

4.7. REFERENCES

Darwin, C.R (1871) The Descent of Man, and Selection in Relation to Sex London: John Murray

Dreiss, A.N & Roulin, A (2014) Divorce in the barn owl: Securing a compatible or better mate entails the cost of re-pairing with a less ornamental female mate Journal of Evolutionary Biology 27, 1114-1124

Fromonteil, S et al (2021) Sexual selection in females across the animal tree of life bioRxiv (https://www.biorxiv.org/content/10.1101/2021.05.25.445581v1.article-info)

Marshall, H.H et al (2021) A veil of ignorance can promote fairness in a mammal society Nature Communications 12, 3717

Okasha, S (2012) Social justice, genomic justice and the veil of ignorance: Harsanyi meets Mendel Economics and Philosophy 28, 1, 143-171

Prazapat, G et al (2022) Males of the parasitoid wasp, Nasonia vitripennis, can identify which fly hosts contain females Royal Society Open Science 9, 211865

Rawls, J (1971) A Theory of Justice Cambridge, MA: Belknap Press

Sten, T.H et al (2021) Sexual arousal gates visual processing during Drosophila courtship Nature 595, 549-553

Valentino, A et al (2021) Reproductive success diminished following mate loss for females but not males in a monogamous rodent Behavioural Processes 188, 104415

Ventura, F et al (2021) Environmental variability directly affects the prevalence of divorce in monogamous albatrosses Proceedings of the Royal Society B 288, 20212112

Wilson, K.M et al (2022) Divorce rate varies with fluidity of passerine social environment Animal Behaviour 183, 51-60

5. VOCAL LEARNING

5.1. OVERVIEW

As far back as the late eighteenth century, Daines Barrington of the Royal Society in London observed that: "Notes in birds are no more innate, than language is in man, and depend entirely upon the matter under which they are bred, as far as their organs will enable them to imitate the sounds which they have frequent opportunities of hearing" (quoted in Vernes et al 2021a).

The study of vocal learning in a systematic way required the development of tape recorders, which expanded the interest beyond birds. "Studying vocal learning in a wide range of animals has the potential to shed light on why it arose so extraordinarily productively in our own recent evolution" (Vernes et al 2021a p1).

How to define and categorise vocal learning? Janik and Slater (2000), for example, distinguished between "vocal usage learning" ("in which existing signals are given in a new context or space") and "vocal production learning" (VPL) ("in which signals are modified in form after experience with the signals of others"; Vernes et al 2021b p2). This difference may be associated with different neural mechanisms, or with shared ones. "A major challenge for future research will be to elucidate the neural mechanisms underlying the different aspects of vocal modifications and vocal learning" (Vernes et al 2021b p9).

Vocal learning involves vocal variation, but there are occasions when such variation is not evidence of learning. For example, animals modifying their signals to compensate for variations in their environments. "One sophisticated phenomenon that involves auditory–vocal feedback but is not generally defined as vocal learning is the Doppler shift compensation (DSC) of Rhinolophid bats. When a bat hears a Doppler-shifted echo, it precisely modifies the frequency of its call so that the echo stays in a preferred frequency band. DSC is achieved by auditory–vocal feedback mechanisms in the midbrain that do not require learning..." (Vernes et al 2021b p2).

Vocalisations can also change without learning due to reproductive state of the animal, stress, arousal, and disease, for instance (Vernes et al 2021b).

Concentrating, firstly, on vocal usage learning, Vernes et al (2021b) outlined its characteristics:

i) "Learning to use calls in a new context" - In laboratory experiments, for instance, animals can be taught to produce vocalisations to conditioned stimuli, while in the wild, an example of this characteristic is the production of alarm calls in the absence of a predator in order for the signaller to gain access to food.

ii) "Learning timing of call use" - eg: duetting songs in birds. "In canebrake wrens (Cantorchilus zeledoni), juveniles start duetting by singing together with adults, and their co-ordination of songs becomes better over time. Furthermore, adults that acquire a new partner have poor co-ordination directly after pairing, but this improves the longer they duet together" (Vernes et al 2021b p4).

iii) Flexibility - eg: grey parrots taught to use human words to refer to objects.

Concerning VPL, Vernes et al (2021b) saw this as "an 'umbrella' term covering a number of behavioural dimensions" (p5):

a) Linked to the auditory model (ie: the signal of others):

- Modification - eg: bottleneck dolphins develop their own signature whistle from whistles heard in their environment.

- Accurate copies - eg: young birds may learn to faithfully imitate the song heard (high fidelity) in some situations like social bonding, as opposed to improvisation (medium fidelity) or an entirely new song (low fidelity) (Beecher and Brenowitz 2005).

b) Linked to the degree of modification:

- Type - "Production learning may involve modifications of existing vocalisations or the production of completely novel vocalisations" (Vernes et al 2021b p5).

- Breadth of learning - eg: lyre-birds can copy sounds of other animals and in the environment (eg: chainsaws).

c) Linked to the timing of learning:

- When.

- Length of time.

- How long the learning is retained - eg: short-term vs long-term retention.

Understanding vocal learning in different species requires understanding the behaviour, mechanisms, and evolution (eg: selection pressures) of it (Vernes et al 2021b).

Colombelli-Negrel et al (2021) observed: "Most so-called 'vocal non-learners' have been classified as non-learners owing to their phylogenetic affinities with other non-learners, or by omission, because we lack experimental tests of their discriminatory or learning capacity" (p1).

5.1.1. Methodology

Lattenkamp et al (2021a) noted: "Among others, VPL has been described as 'matching', 'imitating', 'copying', 'reproducing', 'resembling' and 'vocally mimicking' conspecific, heterospecific or artificially generated acoustic signals. The fickle and varied nature of these descriptions is based in part on the diversity of its expression and, additionally, on the heterogeneity of its measurements" (p1).

These researchers highlighted this concern that different experiments have used the same terms to describe "sometimes drastically different findings" (Lattenkamp et al 2021a p1).

Lattenkamp et al (2021a) outlined some methodological issues, including:

i) VPL is measured in some experiments by an animal's ability to imitate human speech (eg: parrots, songbirds), sometimes after extensive training, sometimes spontaneous mimicry. "A common evaluation strategy is to enlist human raters to either transcribe the recordings or judge acoustic similarity between the recordings and the target sound. Furthermore, it is typical to assess the similarity between tutor and tutee vocalisations based solely on visual inspection of spectrograms" (Lattenkamp et al 2021a p2).

ii) Experimental designs include isolation studies (raising an infant without hearing adult calls), transfer studies (the infant is raised hearing calls of another species), or vocal adjustment in response to playback. These methods have been tried with bats, for example, but the operationalisation of VPL varies between studies. "While some studies focus on the fundamental frequency, others focus on bandwidth, or spectral centroid frequency, or used discriminant function analyses to assess a number of parameters in combination" (Lattenkamp et al 2021a p2).

iii) Establishing a baseline for a species is crucial, as VPL (ie: novel calls) can only only be judged in relation to it. For some species there is a lack of knowledge of the "typical vocal variation" (ie: baseline).

iv) Experimental conditions may limit the parameters of the study - eg: "artificial or natural background noise, constraints within the recording chain (limited sample rate, frequency range of the microphone/hydrophone etc), the acoustic character of the recording site (transmission loss, filtering characteristics, reverb), distance from the sound source, and the observability of the animal under investigation" (Lattenkamp et al 2021a p3).

v) The need for full details of training conditions and durations when animals have been experimentally trained. For example: "Non-reported preliminary studies selecting for good learners blur the actual evaluation of the number of individuals willing and/or able to learn the task. Reporting the overall number of trained individuals does not indicate the species capacity for VPL, but would help to assess the species' overall willingness to learn the VPL task. This could help to select suitable model species and to make decisions about required sample sizes" (Lattenkamp et al 2021a p4).

vi) How the data are analysed - ie: the software or algorithm used.

5.2. SONGBIRDS

There are "4000 plus" species of songbirds (oscines). "Some songbird species tick all the boxes for vocal production learning..., but others fulfil only a subset of the criteria, if that" (Searcy et al 2021 p1) (appendix 5A).

Searcy et al (2021) criticised a binary view of vocal learning as either present in a species or not, and argued for a greater variety of positions.

Four species have been studied the most historically in experiments - chaffinches, white-crowned sparrows, song sparrows, and swamp sparrows (the "canonical species"; Searcy et al 2021) [4]. The experiments include isolating the birds soon after hatching, physically deafening them, or raising them with conspecifics only. The point being to prevent the birds hearing adults of their species sing. Thus, to prevent learning from others. "Although abnormal in many ways, the songs of isolate individuals of our canonical species nevertheless resemble natural song in some respects" (Searcy et al 2021 p2).

There is limited research on other species (Searcy et al 2021).

Searcy et al (2021) proposed the following types of

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[4] The key researchers include Thorp (eg: 1954), Marler (eg: 1970), and Konishi (eg: 1965).

vocal learning in songbirds (building on Tyack 2019):

i) Vocal non-learning - No need to hear other's song for development of own normal song.

ii) Limited vocal learning - Normal song can develop without external models, but hearing others can fine the song.

iii) Complex vocal learning - Normal development requires to hear external models.

5.2.1. Zebra Finch

The zebra finch (Taeniopygia guttata) is a widely experimentally studied songbird. "Only zebra finch males sing, and they learn their song from adult males, including their father. Female zebra finches do not produce learned vocalisations, but they also form a memory of their father's song" (Mol et al 2021 p1).

The basic song has a number of "syllables" (song units separated by brief pause (eg: 10 ms)). It is possible that the order of song syllables may follow certain rules (Mol et al 2021).

Experiments have changed the order of syllables in playback recordings to test perception and recognition. Females show a preference for their father's song over that song with two syllables changed in the middle, for example (Riebel 2000).

Mol et al (2021) developed this research with seventeen male and fifteen female zebra finches. The laboratory-bred birds were raised by their father and mother until seventy days after hatching, and then placed in a single-sex aviary. This gave the opportunity to hear the father's song when young.

Individual birds were given "phonotaxis preference tests". There were two playback speakers, one at each side of the cage, playing different songs, and the orientation/movement of the bird was scored as preference. The choice was between the unchanged father's song (control) and an altered version (middle syllables changed; end syllables switched; or order inverted).

In the baseline condition, the father's song was played opposite a novel song, and all birds preferred the former (ie: spent more time at that side of the cage). This indicated recognition of the father's song heard in early life.

The birds always preferred the normal song to the altered versions with syllables changed. But no preference was shown with the father's song versus the inverted version. This suggested that "syllable order was not a crucial feature for recognition" (Mol et al 2021 p5).

Other studies have found that the father's "voice" is not recognised, so it must be information present in the song. Also, "previous studies have shown that zebra finches do not need to hear all syllables for song recognition, and birds can recognise conspecific songs in which half of the song is deleted. This may be important for zebra finches, as these birds live in large, loud groups in the wild, and song may be partially masked by the song of other birds" (Mol et al 2021 p6). the researchers were left to speculate that spectral features of the song (eg: pitch) are key in recognition.

The study found a difference between males who were the poorest imitators of the father's song and "good imitators" (ie: accurately copied the whole song). When comparing the normal and inverted songs, "poor imitators tended to approach the inversed, and good imitators the normal father's song" (Mol et al 2021 p5). This confirmed that syllable sequence was not important.

5.3. NON-SONGBIRDS

"In addition to parrots and songbirds, evidence for vocal production learning has recently come to light in a number of other bird groups, showing that its occurrence is now more widespread than realised even a few years ago" (Vernes et al 2021 p3). ten Cate (2021) reviewed the evidence on these birds (ie: non-songbirds or non-oscines) (table 5.1).

i) Sub-oscines (about 1400 species) - eg: A bare-throated bellbird housed with a female chopi blackbird as a juvenile produced two different blackbird sounds along with their bellbird basic song (Kroodsma et al 2013).

ii) Woodpeckers and aliies (including 50 species of toucans) - eg: Field observation of mimicking by emerald toucanets by Wagner (1944) not confirmed (ten Cate 2021). "Also, various toucan species are frequently kept as pets but none of the online platforms on which owners exchange information mentions any indication of vocal learning" (ten Cate 2021 p5).

iii) Loons (5 species) - eg: Changes in the yodel call when moving to a different territory, but what drives the change is not known (ten Cate 2021).

iv) Cuckoos (151 species) - eg: The young of some species show the ability to change their begging call to be similar to the host's call (eg: Horsfield's bronze cuckoo).

v) Hummingbirds (365 species) - eg: An isolated laboratory-raised Anna hummingbird produced a poor version of their song, while three individuals raised together had a shared song, suggesting a song model is needed (Baptista and Schuchmann 1990).

vi) Shorebirds (including 101 species of gulls) - eg: Black-headed gulls reared in isolation could not produce the appropriate call (Groothuis 1992).

vii) Landfowl - eg: Deafened chickens developed the normal vocalisations suggesting an absence of vocal learning (Konishi 1963).

viii) Waterfowl (176 domesticated species) - eg: Vocal imitation by a hand-reared Australian musk duck called "Ripper" (appendix 5B).

Grouping of Birds	Modification of Vocalisations	Novel Vocalisations
Sub-oscine	Some	Yes
Woodpeckers and allies	No	Possible
Loons	Some	No
Cuckoos	Some	No
Hummingbirds	Some	Yes
Shorebirds	No	Some
Landfowl	Possible	No
Waterfowl	No	Yes
Parrots	Yes	Yes
Songbirds	Yes	Yes

(Yes = good evidence on all aspects of vocal behaviour; Some = some evidence of some of behaviours; Possible = very little evidence; No = no evidence or no studies)

(Based on table 1 ten Cate 2021)

Table 5.1 - Summary of evidence for two types of VPL in different groupings of birds.

ten Cate (2021) concluded that their overview showed that "the vocal characteristics in a range of species can be affected by experience. The extent of the modifications vary from limited or temporary adjustments, such as modifying an existing vocalisation to become more similar or dissimilar from a vocalisation of a particular conspecific, to producing long-lasting strongly deviating sounds copied from other species or from non-natural sources" (p8). There is, however, a dearth of studies, particularly hand-reared isolation or cross-fostering experiments.

VPL is not a single unidimensional process, and "different mechanisms can result in 'vocal learning', and each of these is present to a larger or lesser degree in distinct branches of the avian phylogeny. This indicates that the presence of vocal learning is the result of convergence from a series of independent evolutionary trajectories originating from different starting points" (ten Cate 2021 p11).

Similar vocalisations by closely related species may have common heritable components (called "phylogenetic signal"). Arato and Fitch (2021) examined 71 songbirds and 66 non-songbirds, and found that "strong phylogenetic signal is present in vocally learned birdsong, as well as songbird calls and non-passerine display vocalisations presumed to be unlearned" (p6).

This suggested to the researchers that "vocal learning is compatible with genetic determination of and/or genetic constraints upon vocalisation structure", and "most interestingly, there may be genetic constraints upon the neural control and/or learning mechanisms themselves, that is on the neural circuitry involved in selecting, imitating and producing vocalisations" (Arato and Fitch 2021 p7).

5.4. PRE-NATAL LEARNING

Colombelli-Negrel et al (2021) studied the response of various avian embryos to calls. The heart rate (HR) of wild eggs were measured, and "a drop in embryonic HR has been shown to reflect physiological mechanisms for orientation and attention" (Colombelli-Negrel et al 2021 p2).

The first experiment involved sixty seconds of silence (baseline), followed 60 seconds of playback (either the calls of an individual of the same or different species), and then sixty seconds of silence again. in total, 109 embryos from four species were tested (superb fairy-wren (Malurus cyaneus) in Australia, Darwin's small ground finch (Geospiza fuliginosa)) on the Galapagos Islands, the little penguin (Eudyptula minor) in Australia and New Zealand, and the Japanese quail (Coturnix japonica domestica)). The first two species are classed as "vocal learners".

All species responded to the conspecific vocalisations, but a larger response was recorded from the "vocal learners". Only the "vocal learners" responded to the heterospecific vocalisations.

The second experiment included three sets of playback conspecific songs inbetween the two bursts of silence. The three playbacks were either from the same individual or different individuals. There were 138 embryos tested from the same four species as the first experiment, and the red-winged fairy-wren (Malurus elegans) (classed as a "vocal learner"). The ability to recognise the same individual singing would produce habituation by the third time (ie: less reduction in HR). All species responded to the first set of vocalisations with lowered HR, and only the quail did not habituate to the third vocalisation from the same individual. This showed that "in general, avian embryos have the capacity to perceive sound and learn a response to sound in ovo. This implies that pre-natal auditory experience may guide an individual's attention to cues experienced pre-hatch (and early post-hatch) and may result in different patterns of attention towards familiar and unfamiliar stimuli" (Colombelli-Negrel et al 2021 p5).

Colombelli-Negrel et al (2021) summed up their findings and the implications: "we showed that embryos of a diverse group of avian species with different characteristics responded more strongly to conspecific vocalisations than to heterospecific vocalisations, and that overall response strength towards conspecific vocalisations was greater in vocal learners than non-learners. By contrast, and contrary to our prediction, we found a similar pattern of habituation response in all species when embryos were exposed to repeated stimuli. The findings of this study suggest that the capacity to perceive and habituate to sound in ovo in developing birds may be more widespread taxonomically than previously considered and also support the idea that vocal perception learning is not a binary behaviour" (p4).

No details were given of the age of the eggs and thus the development of the embryos. Furthermore, species develop at different speeds based on the time spent in ovo. "Precocial embryos (Japanese quail; classified as a vocal non-learner) hatch at a much later relative stage of development compared to semi-altricial (little penguin; classified as a vocal non-learner) or altricial (oscine Maluridae and Geospizidae; classified as vocal learners) offspring" (Colombelli-Negrel et al 2021 p4).

5.5. MAMMALS

A number of different mammals have been trained in experiments or studied in captive situations (appendix 5C), including (Janik and Knornschild 2021):

i) Cetaceans - eg: bottlenose dolphins have been found to produce "individually distinctive signature whistles which are novel and distinctive frequency modulation patterns broadcasting the identity of the caller" (Janik and Knornschild 2021 p3) (table 5.2), as well as copy computer-generated sounds in experiments.

- Oswald et al (2021) analysed the whistles from continuous passive acoustic recordings of short-beaked common dolphins and long-beaked common dolphins off Southern California, USA, from 2017 to 2020. Twenty-four individuals were identified and 1774 of their whistles were grouped into 447 types. From this, 23 parameters of difference were distinguished, and a clear difference was demonstrated between the two species.

- Oswald et al (2021) stated: "Similarities and differences in the whistle repertoires of these two species are likely to have been caused by a variety of interacting factors such as behaviour, group size and social structure, and environment. Little is known about the behaviour and social interactions of these species and data on their distribution is limited. Short- and long-beaked common dolphins overlap in substantial areas of their ranges, however short-beaked common dolphins appear to range further offshore than long-beaked common dolphins. These differences in distribution may have contributed to the development of different whistle repertoires adapted to different environments. It is also possible that the shared whistle types found between the two species in this study are remnants from the common dolphin repertoire before speciation and that oscillatory whistles became more dominant in short-beaked common dolphins as the two species evolved" (p7).

Table 5.2 - Common dolphins.

ii) Pinnipeds - eg: harbour seals able to vary their calls in response to rewards in experiments.

Stansbury and Janik (2021) set up a playback experiment with twelve wild grey seal pups (Halichoerus grypus) on a Scottish island. Pups spend a lot of time together while the mothers are feeding at sea, after the first 2-3 weeks of nursing.

Pup calls were recorded and digitally altered to make them different to natural calls. The pups in 2012 and 2013 were played the recordings from four days old. The calls of the listeners were recorded to see if they imitated the playback calls heard. The number of playback sessions varied between ten to sixteen depending on the individuals, and the approximate number of calls recorded was over 400 each.

"Exposure to playbacks increased the chance of pups producing a call matching the playback sound" (Stansbury and Janik 2021 p4). The control pups (from 2011), who had not heard the playback, matched the stimuli frequencies in 2% of their calls (ie: well below chance).

This showed "a capacity for horizontal cultural transmission", and that "pups adjust their calls to those of other pups" (Stansbury and Janik 2021 p5).

The researchers wondered why the pups showed such vocal learning: "Pup calls are not part of the adult repertoire and pups stay relatively stationary on land throughout their infancy so that group recognition is not a likely explanation... However, learning may also affect the development of the adult repertoire so that learned variation in pup calls may just be a by-product or early manifestation of learning abilities relevant for the development of adult repertoires. Adult female grey seals tend to associate across seasons and there is evidence for mate fidelity. Learned call conformity may help to maintain such relationships and to facilitate recognition" (Stansbury and Janik 2021 p5) (appendix 5D) [5].

iii) Elephants - eg: an Asian elephant copying human speech sounds in a zoo (Stoeger et al 2012), by using "its trunk to change the shape of its mouth cavity to copy human vowels" (Janik and Knornschild 2021 p5).

Stoeger and Baotic (2021) showed that African elephants were capable of producing sounds in response to verbal cues. Thirteen elephants were observed in five captive facilities. During training positive reinforcements with food rewards and/or praise were used.

Rumbles, trumpets and snorts were produced in

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[5] Hoeksema et al (2021) performed brain scans on two female juvenile grey seals. It was found that the brains were larger than many terrestrial carnivores, with a large cerebellum and temporal lobe. This suggests vocal learning capacity (appendix 5F).

response to verbal cues from the trainers. One adult male, "Jabu", produced seven different vocalisations on cue.

Stoeger and Baotic (2021) commented: "The trumpet seems particularly difficult for elephants to produce on cue. For an elephant to trumpet naturally, context needs to be linked to a specific internal state. Elephants trumpet in situations such as bonding ceremonies... or play behaviour if in a state of high arousal (ie: a trumpet is not always associated with greeting or play). Accordingly, when trumpeting on cue, the elephant probably must co-ordinate brain regions associated with the arousal regulation of vocal production and the pathway involved in volitional vocal control. This potential cognitive effort might be reflected by the observation that the elephants need a considerable time (up to 17 s in one training session by Jabu...) to execute the trumpet" (p5).

Another interesting observation was that "[V]ocalisations on cue never elicited a behavioural response by group members close by" (Stoeger and Baotic 2021 p5).

iv) Bats - eg: training bats to match the frequency of their calls to those of an auditory target, and deafening experiments (appendix 5E).

v) Primates - eg: "Koko" (a western lowland gorilla) raised by humans without other gorillas produced unique sounds (Perlman and Clark 2015).

VPL as an example of social learning has been most studied in birds (and some mammals). Zandberg et al (2021) reported the example of humpback whales.

Within a population males will sing the same song for a while (known as a "song type"). "At the same time, however, the song is also constantly evolving; males incorporate changes into the population song in their own display to maintain the observed conformity. Slow, progressive song evolution is a key feature of all humpback whale populations worldwide" (Zandberg et al 2021 p2). Song sharing between populations can occur if males from different populations meet in a wintering ground, say.

But in 1996 and 1997, something different was observed by researchers. "Song from the west Australian humpback whale population, located in the Indian Ocean, appeared in the east Australian population, in the South Pacific, and rapidly replaced the very different existing song. This process, in which the song in a population is rapidly replaced by a completely novel song, was termed a 'song revolution', to distinguish it from the much slower process of song evolution The new song first appeared in low numbers and then increased in frequency until the old song was completely gone; a process that took 2 years" (Zandberg et al 2021 p2). The reason may have been "a sexually selected drive for novelty" (Zandberg et al 2021 p2).

Using data on 798 songs recorded between 1998 and 2008 in different South Pacific populations, Zandberg et al (2021) developed models to explain song changes. They found that "rare interactions between populations combined with a song memory and a tendency to learn novel songs was sufficient to create patterns of song evolution and revolutions" (Zandberg et al 2021 p8).

Zandberg et al (2021) reflected: "The humpback whale song transmission patterns, as found in the Southern Hemisphere, are unique among non-human animals. While song cultural evolution and local dialects are widely documented in birds, to our knowledge no other species shows a dynamic in which a whole population rapidly and concertedly replaces its song for a different version. Some bird species such as the corn bunting and the village indigobird show a similar pattern of concerted change among all males of a local song dialect" (p10).

5.6. LOMBARD EFFECT

Vocal plasticity allows the animal to adjust its vocal signals to changes in the environment, as in the "Lombard Effect". "Many animal species increase the amplitude levels of their vocalisations in the presence of masking noise to 'sound louder', especially when the noise overlaps with the spectral composition of the species-typical vocalisation" (Torres Borda et al 2021 p2).

Torres Borda et al (2021) explored this effect with eight wild-born 7-10 day-old harbour seal pups (Phoca vitulina) at a seal rescue centre in the Netherlands. Five-minute bursts of audio recordings of normal ambient sounds, like wind, were played at different volumes (65 and 45 dB, and no playback), and the pups' vocal responses were recorded. The seals showed evidence of changing their calls as the noise level increased. In the high noise condition, the fundamental frequency (F_0) was lower as compared to no playback. Number of calls and duration of calls did not vary with background noise level, however.

Torres Borda et al (2021) speculated about the findings: "First, it may be an adaptation to the actual environmental noise that pups encounter: as lower frequencies propagate better in wind, shifting F_0 downwards may increase the travel distance of calls. Second, lowering of the F_0 may be away for seal pups to better communicate their identity" (p7). The F_0 change cannot be explained as an automatic adaptation as "arousal can lead to tension of the vocal folds, inducing an increase in vibration frequency and producing, in turn, an increase in F_0" (Torres Borda et al 2021 p7). Therefore, the pups were showing vocal control, and at a young age.

5.7. BABBLING

Animals that have an extensive vocal repertoire have a developmental period of "practice" before the adult vocalisations. This is called babbling in humans, and this has been applied to non-human species also. ter Haar et al (2021) used the following definition: "babbling is an exploratory stage in vocal development marked by many variable and repetitive vocalisations, for which production does not require a specific social or functional context, suggesting exploration" (p2).

Fitch (2019) proposed that babbling is a pre-requisite for complex vocal learning. This means that all VPL species should have babbling, and non-learners will not. ter Haar et al (2021) considered the evidence among different non-human species:

i) Birds - Bird song in early development is variable (called "sub-song"), then rhythmic sequences of the basic adult song appear ("reminiscent of human pre-canonical babbling" [ie: before syllables]; ter Haar et al 2021 p4). ter Haar et al (2021) summed up: "Babbling-like utterances have been described for many avian species; we are not aware of any songbird species that does not show some form of babbling-like precursor to the song. In fact, even some songbirds that are not generally known to sing, such as female canaries (Serinus canaria), have been shown to occasionally produce vocalisations that are structurally similar to sub-song throughout life" (p4).

ii) Bats - Initially, isolation calls are made after birth, but "babbling bouts" appear at two weeks old (eg:

greater sac-winged bat).

iii) Otters - "In giant otters, babbling probably constitutes motor practice (even though it is currently unknown if VPL occurs) and may also have the advantage of eliciting care from group members" (ter Haar et al 2021 p5).

iv) Other mammals - eg: bottleneck dolphins produce vocal behaviours that "could potentially be classified as babbling" (ter Haar et al 2021 p5).

v) New World primates - eg: documented in two species of marmosets.

ter Haar et al (2021) commented: "There are notable similarities across these species in the developmental pattern of vocalisations, suggesting that vocal production learning might require babbling. However, the current state of the literature is insufficient to confirm this suggestion" (p1). An interesting question, among many, for future research is whether babbling appeared before or after VPL in evolution (ter Haar et al 2021).

5.8. PROTOPHONES

Oller et al (2021) rejected comparative studies in order to understand human language. They said: "The earliest vocalisations in humans reveal foundations required for language to develop, foundations that are weak or missing in vocalisations of our non-human relatives. Because of the foundational nature of early development, we view comparisons in infancy as more instructive about the origin of language than comparisons of mature human language with vocal communication of other primates at any age" (Oller et al 2021 p1).

In particular, human infants, along with cries and screams, and laughs, produce "protophones". These include "both non-canonical (eg: squeals, growls and vowel-like sounds) and canonical babbling (consisting of canonical syllables such as ‘ba' or ‘da’ and sequences, ‘baba’ or ‘dada’ and so on)" (Oller et al 2021 p2). It is becoming clear that protophones are the most common vocalisations by babies, outnumbering cries (Oller et al 2021).

Protophones appear to be "largely endogenous" (ie: without social learning). So, "the predominantly endogenous driving of the protophones suggests that learning of vocal production categories during the first year may be primarily a result of self-organisation, a consequence of infant exploration rather than of learning through input from caregivers" (Oller et al 2021 p2). This is challenging to the theories of language acquisition that emphasise the importance of social interaction and imitation.

Oller et al (2021) provided supportive data from language recordings of infants in the USA. For fifty-three infants, nine all-day recordings were collected in the first year of life, and the type of vocalisations quantified. Between 6-12 months old, protophones outnumbered cry/whimpers (74 times more frequently), and these outnumbered laughs (eight times more frequent). All-day recordings of twelve more infants in a playroom situation confirmed the patterns.

Protophone production occurred equally in the presence or absence of an adult, while laughter and cry/whimper were either in situations of social interactions or distress. Oller et al (2021) saw protophones as "vocal functional flexibility" (VFF) (ie: "the ability to produce a set of particular sounds freely in any emotional state is clearly a foundation without which learning to use a word would be impossible"; pp5-6). The other vocalisations did not show VFF.

Oller et al (2021) asked two questions: "Why, then, do protophones exist at all? And why do they occur so frequently compared with crying and laughter?" (p7). They continued: "The questions are not trivial because it can be assumed that the ability to produce sounds with VFF must have preceded the origin of vocal language. Consequently, at their earliest appearance in hominin evolution, vocalisations with VFF must have been selected for in accord with pressures that had nothing to do with language, which did not yet exist" (Oller et al 2021 p7). The authors made a comparison with cry/whimper and laughter: "Both these types of vocalisations express definable emotional states and serve definable and relatively consistent functions that have direct potential benefits at the moment they are produced. Cry/whimpers signal need for care, and laughter signals playful social connection. It seems straightforward to postulate that mammals, being dependent on maternal care, are under selection pressure to have the ability to produce these kinds of sounds as needed" (Oller et al 2021 p7).

Continuing their speculation on the evolution of protophones, Oller et al (2021) argued that they are fitness signals - ie: "protophones predominantly supply information about infant wellness even to caregivers who are busy doing something else nearby" (p7). This is important because human infants are dependent on caregivers for longer periods than other primates, and ancient hominin groups were larger than those of other apes, probably including co-operative breeding and alloparenting. So, "infants could profit from broadcasting fitness indicators in the competition for care for a variety of alloparents" (Oller et al 2021 p7).

5.9. VOICE MODULATION

"Although human speech is often thought to be categorically different from non-human animal vocal communication, many aspects of human acoustic communication are directly comparable with those of other land vertebrates. These include both the vocal apparatus itself and the main voice modulatory cues involved in vocal production" (Matzinger and Fitch 2021).

Voice modulatory cues include variations in fundamental frequency, duration and pauses, and are found in human and non-human vocalisations in both common and different ways. Common to all are vocal tract anatomy and respiratory constraints that influence the modulation. Vocal signals involve a source and a filter.

Firstly, "a source generates acoustic energy using an airflow from the lungs. This source is the larynx in most tetrapods and the syrinx in birds, and consists of vibrating tissue that creates sound by oscillating at a particular rate termed the fundamental frequency... This source signal is then filtered in the supra-laryngeal vocal tract (upper respiratory tract) via multiple formant frequencies that act as a series of bandpass filters, attenuating or enhancing certain frequency ranges. The actual vocal output fuses these two components (source and filter)..." (Matzinger and Fitch 2021 p2).

A common observation about vocalisations in animals is that larger animals produce lower frequency sounds. This allometric scaling is taken as an honest signal of size. However, it has been proposed that vocal plasticity (or VPL) evolved as a way to cheat this signal (Garcia and Ravignani 2020).

Ravignani and Garcia (2021) explored this idea further by analysing various mammalian species. Contrary to Garcia and Ravignani (2020), they did not find a simple relationship between vocal plasticity and allometry-cheating vocalisations. This suggested that different selection pressures influenced vocal plasticity and allometry-cheating strategies.

5.10. COMPARATIVE STUDIES

Human vowel sounds require lip, tongue and jaw articulation movements as well as supra-laryngeal articulations. Studying the different calls of non-human primates and their physical articulations can help in understanding the origin of human speech.

Grawunder et al (2021) reported data from the Tai Chimpanzee Project in the Ivory Coast between 2013 and 2016, which included the vocalisations of twenty-eight adult and sub-adult chimpanzees. Video recordings were analysed for physical articulations, and a scoring system was devised for jaw and lip positions.

Four broad call types (hoos, grunts, barks, and screams) were distinguished based on acoustic analysis, and on visual articulations. Concentrating on vowel sounds, it was found that "chimpanzees share both a larger and more overlapping vowel space with humans than monkeys species. Presumably the capacity to generate a larger vowel space creates the potential to create more divergent vocal signals and hence more diverse vocal messages" (Grawunder et al 2021 p9). There was enough difference, however, to suggest "moderate evolutionary change... continuing through hominoid evolution" (Grawunder et al 2021 p1).

5.10.1. Dominance Style

Many animals live in asymmetrical dominance relationships or dominance hierarchies. In this situation, the dominant individual may be "despotic" or "tolerant". This describes the degree to which the dominant individual asserts their dominance (Kavanagh et al 2021).

Kavanagh et al (2021) investigated vocalisation in relation to dominance style. It was predicted that there would be greater communication where the dominant partner was tolerant than despotic. The researchers analysed data from 111 studied wild groups of twenty-six non-human primate species. Because the data came from different sources a dominance style score was created (based on the means of the species). Dominance was based on observed aggressive behaviour during feeding, for instance. Vocal communication was scored as number of vocalisations, overall repertoire size, and number of hierarchy-related calls in the repertoire. "Calls described as occurring in an appeasement or dominance context were classed as hierarchy-related signals" (Kavanagh et al 2021 p7).

Focusing on the individual level within a species, it was found that "dominant individuals who were more tolerant vocalised at a higher rate than their despotic counterparts. This indicates that tolerance within a relationship may place pressure on the dominant partner to communicate more during social interactions" (Kavanagh et al 2021 p3). Subordinate individuals did not vocalise more or less frequently depending on the dominant individual's style. But comparing the animals at a species level, "despotic species exhibited a larger repertoire of hierarchy-related vocalisations than their tolerant counterparts" (Kavanagh et al 2021 p3).

Though the findings appear contradictory, the important point for the researchers was that "the strictness of the dominance relationships of individuals and species provide important context for understanding primate vocal usage and evolution" (Kavanagh et al 2021 p11).

Kavanagh et al (2021) accepted "the caveat that more validation of dominance style measures across primate species is needed to confirm the validity of our findings. Ours is the first attempt to measure dominance style on a continuous scale across the primate order, so it is perhaps not surprising that we did not find that all dominance style measures predicted communication in our sample" (p12). Non-verbal communication was not measured, and "some species or individuals may rely more heavily on facial, gestural or olfactory communication than vocal signals. A more holistic, multi-modal approach to characterising communication in future would, therefore, be beneficial" (Kavanagh et al 2021 p13).

5.11. MISCELLANEOUS

Human music is separate to language, but there may be common origins and elements. For example, calls with song-like structures help to localise individuals in relation to each other in dense forests. "A lack of clarity concerning the whats (outcomes and inputs) and hows (level, unit, tempo, and mode) of the evolution of musicality, however, has thus far stifled rigorous testing of origin theories" (Schruth et al 2021 p2).

Schruth et al (2021) proposed a "locomotion-based hypothesis" for the origins of proto-musicality - ie: "spatio-temporal precision in landing during perilous arboreal locomotion favoured the evolution of musical calling in early primates - vastly preceding the origin of more music-like behaviour in hominoids and subsequent emergence of music in later hominids" (p1). Put simply, aerial locomotion through dense forests (eg: leaping and swinging) co-evolved with "song-like proto-musical calling". The researchers analysed 832 vocalisations from sixty primate species, and locomotion data from 112 species.

5.11.1. Tamarin Calls

Selection pressure can produce convergent or divergent traits. For example, pressure to avoid incest increases differences between individuals raised together, while group membership recognition favours similarity to avoid aggression towards outsiders.

Sobroza et al (2021) focused on calls used as a defensive resource towards territorial intruders. Neighbours may have similar calls to avoid aggression (eg: bird species). On the other hand, characteristics of the environment may influence the evolution of calls (eg: long, low-pitched calls in woody forests). This is particularly important in human-modified landscapes.

In Central Amazonia (Brazil), the red-handed tamarin (Saguinas midas) and the pied tamarin (Saguinas bicolor) are closely related inhabitants (figure 5.1). Sobroza et al (2021) investigated the similarity of their territorial calls at eight sites. Recordings were made of 275 calls over 97 days in 2014-15. Calls were scored for similarity on different variables like frequency (kHz), bandwidth (ie: difference between lower and upper frequency), and number of elements (syllables) of the call.

It was predicted that selection pressures would favour convergence of territorial calls if there was a risk of conflict. There was partial support for this prediction. There was convergence with red-handed tamarins shifting their calls towards the pied tamarins' acoustic pattern, but only in "old-growth (primary or pristine) forests". These "tend to be more complex in terms of canopy stratification, having larger and taller trunks and more closed canopy..., all of which could affect sound propagation" (Sobroza et al 2021 p2). In "secondary forests" (ie: areas affected by human modification in recent years), the red-handed tamarin calls were not similar to pied tamarins, and were adapted to optimise sound propagation.

These findings suggested that territorial calls were influenced by social (eg: neighbours) and environmental (eg: human modification) pressures. Sobroza et al (2021) warned: "As their effects can interact, analyses, which assume that these ecological pressures act independently, are likely to miss important patterns" (p1).

(a) Red-handed tamarin

(b) Pied tamarin

(Source: (a) Mathias Appel (in public domain); (b) Cedricguppy - Loury Cedric)

Figure 5.1 - Red-handed and pied tamarin.

5.11.2. Plain-Tailed Wren

Plain-tailed wrens (Pheugopedious euophrys) (figure 5.2) sing by themselves and in male-female duets as both sexes sing. "During duets, female and male plain-tailed wrens take turns, alternating syllables at a rate of between 2 and 5 Hz" (Coleman et al 2021 p1).

Solo and duet singing is different. In solo singing, the bird hears only its own vocalisations (autogenous feedback), while in duet singing there is also heterogenous feedback (hearing the other singer's song as well). Coleman et al (2021) were interested in the integration of heterogenous and autogenous feedback in the brain (ie: the song control area HVC). "HVC is necessary for song learning, production, and timing in species of songbirds that do not perform duets. Neurons in HVC are active during singing and respond to playback of the bird's own learned song. In addition, recent work has shown that HVC is also involved in vocal turn taking" (Coleman et al 2021 p1).

Four pairs of wrens were studied by surgically implanting electrodes into the HVC which measured neuronal activity. HVC activity increased during a bird's song production in the duet (autogenous feedback), but decreased when the partner was singing (heterogenous feedback). Hearing a partner's song inhibits HVC activity.

This study, which was typical of those investigating animal physiology, showed both the good and bad of animal welfare. Wild birds were caught in mist nets, kept in good conditions, had brain surgery, and were euthanised after the research.

(Source: Browerk; licensed as https://creativecommons.org/licenses/by-sa/3.0)

Figure 5.2 - Plain-tailed wren.

5.12. APPENDIX 5A - SONGBIRDS

Songbirds appear to have an extra chromosome not found in other birds (Wong 2019). It is called the germline-restricted chromosome (GRC), and is only present in reproductive cells, but is only transmitted to offspring via the mother (Wong 2019).

Torgasheva et al (2019) established the existence of GRC in songbirds in a study of sixteen varied species of songbirds and eight of non-songbirds.

It is speculated that GRC is involved in the development of sperm and eggs in the breeding season (Kinsella et al 2019). "Birds need additional copies of germ-cell-specific genes for a very short breeding period only to produce a lot of sperm and load [egg cells] with large amounts of proteins. They have no reason to carry these genes throughout the year and in [the rest of the body's] cells when and where they are of no use" (Pavel Borodin in Wong 2019).

The finding of the GRC has implications for understanding other organisms (Wong 2019).

5.13. APPENDIX 5B - AUSTRALIAN MUSK DUCK

"Ripper" was a male captive-reared Australian musk duck (Biziura lobata) (figure 5.3) who was recorded in 1987, and these recordings were supplemented by those of a captive male in 2000 (ten Cate and Fullager 2021).

(Source: JJ Harrison; https://en.wikipedia.org/wiki/User:JJ_Harrison_rdfrom=commons:User:JJ_Harrison)

Figure 5.3 - Australian musk duck.

Three types of imitation by Ripper were recorded [6]:

i) Slamming door (close to where the duck was raised).

ii) Slamming door and speech-like mumble (but no clear words discernible).

iii) Speech-like phrase, which could be "you bloody fool" or "you bloody food". "The vocalisation is most

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[6] Audio recordings at https://www.youtube.com/watch?v=b_hmu2p1DYc (accessed 23rd November 2021).

likely an imitation of a phrase he heard repeatedly from his caretaker, but it is not known at which age he was exposed to it" (ten Cate and Fullager 2021 p4).

The other duck was recorded making a "whistle-kick" vocalisation, and imitating the Pacific black duck. The former is usually made by males as put of displays. "The whistle-kick consists of a non-vocal splash component produced by the feet hitting the water, followed by two distinct vocal components: a soft low-frequency sound followed by a much louder whistle" (ten Cate and Fullager 2021 p2).

ten Cate and Fullager (2021) felt that the recordings "indicate the vocal development of the musk duck fits the various criteria used as evidence for vocal production learning in songbirds, parrots and hummingbirds" (p5).

There was a lack of background information about the two cases reported in order to know the age of exposure to the sounds. With Ripper, the "recordings were made at 4 years of age and a comment stated that the sounds were only recently noticed by the caretaker. Whether there is a sensitive phase for learning cannot be assessed from the current data. In the wild, musk ducks would easily hear males from the time of hatching, as males would be calling in the area" (ten Cate and Fullager 2021 p6).

ten Cate and Fullager (2021) reflected on two key issues:

a) What do the cases say about the evolution of VPL in birds? "One hypothesis is that vocal learning evolved once in the common ancestor of the taxa showing vocal learning, followed by subsequent losses in vocal non-learning taxa, while an alternative one is that it arose in various groups independently" (ten Cate and Fullager 2021 p5).

ten Cate and Fullager (2021) continued: "The musk duck belongs to a basal clade in the avian phylogeny. Thus, if vocal learning evolved only once this must have been almost at the root of the avian tree with subsequent losses in many branches. We consider this less likely than the scenario of several independent origins" (p5).

b) Why would musk ducks have vocal learning when it is not present in closely related (Anserinae) species? Musk ducks are highly altricial, which means a long period after hatching spent with the mother while developing, and there are relatively few offspring per season. "Being altricial, the longer period of dependency might also be accompanied by a more gradual development of neural systems, providing the scope for a larger impact of experience (learning) on behavioural development" (ten Cate and Fullager 2021 p8).

Another relevant factor may be that musk ducks are a lekking species. Males gather in one place and competitively display to females who come to the lek, mate, and nest elsewhere. So, there is an "incentive" for males to have ways to "stand out from the crowd", of which unique vocalisations could be one way. Not enough is known about this species at this time. Non-vocal displays are the norm (ten Cate and Fullager 2021).

5.14. APPENDIX 5C - CAPTIVE VS WILD

Animals in captivity may be different to their wild counterparts. "For social animals, housing and husbandry may have more far reaching consequences, altering not just the behaviour of individuals but also the more general social structure of captive animal groups" (Pacheco and Madden 2021 p1).

Meerkats are a good species to study in terms of their social networks because detailed observations of free-living communities exist (eg: Madden et al 2011).

Using the definitions of Madden et al (2011), Pacheco and Madden (2021) studied captive groups of meerkats in zoological parks in the UK and Mexico in relation to foraging competitions, grooming, and dominance interactions. A total of 113 individuals in fifteen groups were observed for twenty hours per group.

The researchers showed differences "to some degree" between the captive groups and those studied in the wild. Put simply, the captive animals had a tighter social network, "representing a greater interaction of wild individuals with the majority of all other members of the group than captive individuals" (Pacheco and Madden 2021 p4). For example, grooming interactions were more egalitarian in the wild, whereas in the captive meerkats, there was "a more highly skewed grooming distribution with a small number of individuals being recipients to a large number of grooming interactions" (Pacheco and Madden 2021 p5).

Dominance interactions also differed, as did foraging competitions in subtle ways.

Pacheco and Madden (2021) ended that their study "does not generalise the results beyond the particular groups of meerkats studied here. Nonetheless, the results show how the social interaction of captive meerkats may vary from their wild counterparts and that such variation in the degree to which members of the group interact with one another could be due social and non-social factors. Particularly, the current results suggest that a meerkat social network in captive conditions can be less consistent than in their wild environment in the way they associate with one another, and in the manner they occupy particular positions in the network" (p7).

5.15. APPENDIX 5D - CALL RECOGNITION

Linossier et al's (2021) playback experiments with northern elephant seals (Mirounga angustirostris) found mothers recognised their offspring's call at a very young age.

The animals were studied in the wild (in California), and the researchers recorded pup vocalisations first. Then 22 mothers were tested at 1-2 days, and 1, 2, and 3 weeks after birth. The playback involved the focal female's own pup or a non-related pup of a similar age. Observers, blind to the playback condition, scored the response of the mother (table 5.3).

Mothers always responded more strongly to the vocalisations of their pups than others (eg: moved faster towards the playback speaker or called more quickly in response). Recognition of own pup's call was evident at 1-2 days old.

So, if mothers nurse pups that are not their own, which has been observed (eg: Riedman and Le Boeuf 1982), it is not due to "deficient vocal recognition" (Linossier et al 2021 p3).

- Latency to look towards the playback speaker (seconds)
- Latency to move towards the speaker (secs)
- Latency to vocalise in reply (secs)
- Latency to touch the speaker (secs)
- Latency to sniff the speaker (secs)
- Number of vocalisations in one minute after playback onset

All the variables combined to give a "response strength score" (out of 6)

Table 5.3 - Six behavioural variables of maternal response scored by researchers.

5.16. APPENDIX 5E - DEAFENING EXPERIMENTS

Vocal learning has been investigated in deafening experiments, where the animal cannot hear other calls. Lattenkamp et al (2021b) reported one such experiment with peak spear-nosed bats (Phyllostomus discolor). Three bats at a breeding colony in Germany were deafened by auditory overstimulation at less than two weeks old (table 5.4). Regular recordings of the calls of these bats and three age-matched controls were made for the next six months. The bats were also studied as adults (at three years old).

- "The deafening was performed by presenting the anaesthetised bats with intense (140 dB peak-equivalent sound pressure level) frequency modulated sweeps (1–45 kHz) played back in a continuous loop for 2 h" (Lattenkamp et al 2021b p2).

Table 5.4 - Details of deafening process.

The calls were compared on five vocal parameters from over 100 hours of recordings:

i) Vocal activity - The deafened bats produced significantly more calls at all ages studied (mean 17 vs 1.7 per 10-second period).

ii) Amplitude - "During development, vocalisation amplitude of the deafened juveniles was generally lower than that of the hearing bats, but increased steadily over the recording period. In adulthood, the vocal amplitudes were similar again" (Lattenkamp et al 2021b p3).

iii) Duration - Call duration was shorter among the deafened bats, but not statistically significantly.

iv) Fundamental frequency (or pitch) - This was similar for both groups (15-20 kHz).

v) Aperiodicity (or spectral roughness or irregularity) - There was no difference overall.

Lattenkamp et al (2021b) explained: "If deafened animals display normal vocal development this demonstrates that auditory input is not necessary to shape their vocal repertoire and rules out vocal production learning. On the other hand, while the deafened pale spear-nosed bats did display modified vocal development, this does not conclusively prove the occurrence of vocal learning in this species, until other effects of deafening, such as reduced social interactions and stress, can be ruled out" (p3). It should be noted that deafening experiments with animals that do not show VPL have found increased vocal activity (eg: guinea pigs; Arch-Tirado et al 2000) (Lattenkamp et al 2021b).

The best interpretation of the findings is that bats can produce vocalisations without auditory feedback, but it is a "limited vocal repertoire", and so feedback is "required for fine tuning of vocal emissions" (Lattenkamp et al 2021b p4).

5.17. APPENDIX 5F - HUMAN BRAIN

"Speech production is a uniquely complex human behaviour that requires numerous brain regions to perceive, process and comprehend the sensory input, integrate it with cognitive and motor intent, and execute the synchronised movement of over 100 oro-facial, laryngeal and respiratory muscles" (Valeriani and Simonyan 2021 p1).

This is shown by work by Valeriani and Simonyan (2021), who asked thirty-six native-English-speaking adults to produce meaningful sentences and meaningless syllables while in a brain scanner. A "syllable production network" (SylPN) involving three "neural communities" was distinguished, and a "speech production network" (SPN), which was more complex and involved four neural communities. There was some sharing of brain areas by the two networks.

The SPN (ie: meaningful speech as opposed to meaningless sounds) involved "a highly complex orchestration of brain regional connectivity [...] regulated by a directed neural network, the most influential nodes of which are centred around primary sensori-motor and parietal cortical areas and preferentially influence pre-frontal regions via long-ranging functional connectivity" (Valeriani and Simonyan 2021 p9). Valeriani and Simonyan (2021) continued: "By contrast, the neural network during simpler syllable production is characterised by a more compressed, cost-efficient structure, which supports the essential elements of sequence timing and sensorimotor integration via the influence exerted by superior parietal and cerebellar network hubs" (p11).

5.18. REFERENCES

Arato, J & Fitch, W.T (2021) Phylogenetic signal in the vocal learning and vocal non-learning of birds Philosophical Transactions of the Royal Society 376, 20200241

Arch-Tirado, E et al (2000) Development of isolation-induced vocal behaviour in normal-hearing and deafened guinea pig infants Journal of Speech, Language and Hearing Research 43, 2, 432-440

Baptista, L.F & Schuchmann, K.L (1990) Song learning in the Anna hummingbird (Calypte anna) Ethology 84, 15-26

Barrington, D (1773) Experiments and observations on the singing of birds Philosophical Transactions of the Royal Society 63, 249-291

Beecher, M.D & Brenowitz, E.A (2005) Functional aspects of song learning in songbirds Trends in Ecology and Evolution 20, 143-149

Coleman, M.J et al (2021) Neurophysiological co-ordination of duet singing Proceedings of the National Academy of Sciences, USA 118, 23, e2018188118

Colombelli-Negrel, D et al (2021) Pre-natal auditory learning in avian vocal learners and non-learners Philosophical Transactions of the Royal Society 376, 20200247

Fitch, W.T (2019) Sequence and hierarchy in vocal rhythms and phonology Annals of the New York Academy of Sciences 1453, 1, 29-46

Garcia, M & Ravignani, A (2020) Acoustic allometry and vocal learning in mammals Biology Letters 16, 20200081

Grawunder, S et al (2021) Chimpanzee vowel-like sounds and voice quality suggest formant space expansion through the hominoid lineage Philosophical Transactions of the Royal Society 376, 20200455

Groothuis, T (1992) The influence of social experience on the development and fixation of the form of displays in the black-headed gull Animal Behaviour 43, 1-14

Hoeksema, N et al (2021) Neuroanatomy of the grey seal brain: Bringing pinnipeds into the neurobiological study of vocal learning Philosophical Transactions of the Royal Society 376, 20200252

Janik, V.M & Knornschild, M (2021) Vocal production learning in mammals revisited Philosophical Transactions of the Royal Society 376, 20200244

Janik, V.M & Slater, P.J.B (2000) The different roles of social learning in vocal communication Animal Behaviour 60, 1-11

Kavanagh, E et al (2021) Dominance style is a key predictor of vocal use and evolution across non-human primates Royal Society Open Science 8, 210873

Kinsella, C.M et al (2019) Programmed DNA elimination of germline development genes in songbirds Nature Communication 10, article 5468

Konishi, M (1963) The role of auditory feedback in the vocal behaviour of the domestic fowl Ethology 20, 349-367

Konishi, M (1965) The role of auditory feedback in the control of vocalisation in the white-crowned sparrow Zeitschrift fur Tierpsychologie 22, 770-783

Kroodsma, D et al (2013) Behavioural evidence for song learning in the sub-oscine bellbirds (Procnias spp; Cotingidae) The Wilson Journal of Ornithology 125, 1, 1-14

Lattenkamp, E.Z et al (2021a) A researcher's guide to the comparative assessment of vocal production learning Philosophical Transactions of the Royal Society 376, 20200237

Lattenkamp, E.Z et al (2021b) The vocal development of the pale spear-headed bat is dependent on auditory feedback Philosophical Transactions of the Royal Society 376, 20200253

Linossier, J et al (2021) Maternal responses to pup calls in a high-cost lactation species Biology Letters 17, 20210469

Madden, J.R et al (2011) The social network structure of a wild meerkat population: 3. Position of individuals within networks Behavioural Ecology and Sociobiology 65, 10, 1857-1871

Marler, P (1970) A comparative approach to vocal learning: Song development in white-crowned sparrows Journal of Comparative Physiology and Psychology 71, 1-25

Matzinger, T & Fitch, W.T (2021) Voice modulatory cues to structure across languages and species Philosophical Transactions of the Royal Society 376, 20200393

Mol, C et al (2021) Vocal learning in songbirds: The role of syllable order in song recognition Philosophical Transactions of the Royal Society 376, 20200248

Oller, D.K et al (2021) Protophones, the precursors to speech, dominate the human infant vocal landscape Philosophical Transactions of the Royal Society 376, 20200255

Oswald, J.N et al (2021) Species information in whistle frequency modulation patterns of common dolphins Philosophical Transactions of the Royal Society 376, 20200046

Pacheco, X.P & Madden, J.R (2021) Does the social network structure of wild animal populations differ from that of animals in captivity? Behavioural Processes 190, 104446

Perlman, M & Clark, N (2015) Learned vocal and breathing behaviour in an enculturated gorilla Animal Cognition 18, 1165-1179

Ravignani, A & Garcia, M (2021) A cross-species framework to identify vocal learning abilities in mammals Philosophical

Transactions of the Royal Society 376, 20200394

Riebel, K (2000) Early exposure leads to repeatable preferences for male song in female zebra finches Proceedings of the Royal Society B 267, 2553-2558

Riedman, M.L & Le Boeuf, B.J (1982) Mother-pup separation and adoption in northern elephant seals Behavioural Ecology and Sociobiology 11, 203-215

Schruth, D.M et al (2021) Evolution of primate proto-musicality via locomotion bioRxiv (https://www.biorxiv.org/content/10.1101/2020.12.29.424766v4)

Searcy, W.A et al (2021) Variation in vocal production learning across songbirds Philosophical Transactions of the Royal Society 376, 20200257

Sobroza, T.V et al (2021) Convergent character displacement in sympatric tamarin calls (Saguinus spp) Behavioural Ecology and Sociobiology 75, 88

Stansbury, A.L & Janik, V.M (2021) The role of vocal learning in call acquisition of wild grey seal pups Philosophical Transactions of the Royal Society 376, 20200251

Stoeger, A.S & Baotic, A (2021) Operant control and call usage learning in African elephants Philosophical Transactions of the Royal Society 376, 20200254

Stoeger, A.S et al (2012) An Asian elephant imitates human speech Current Biology 22, 2144-2148

ten Cate, C (2021) Re-evaluating vocal production learning in non-oscine birds Philosophical Transactions of the Royal Society 376, 20200249

ten Cate, C & Fullager, P.J (2021) Vocal imitations and production learning by Australian musk ducks (Biziura lobata) Philosophical Transactions of the Royal Society 376, 20200243

ter Haar, S.M et al (2021) Cross-species parallels in babbling: Animals and algorithms Philosophical Transactions of the Royal Society 376, 20200239

Thorp, W.H (1954) The process of song-learning in the chaffinch as studied by means of the sound spectrograph Nature 173, 465-469

Torgasheva, A et al (2019) Germline-restricted chromosome is widespread among songbirds Proceedings of the National Academy of Sciences, USA 116, 24, 11845-11850

Torres Borda, L et al (2021) Vocal plasticity in harbour seal pups Philosophical Transactions of the Royal Society 376, 20200456

Tyack, P.L (2019) A taxonomy of vocal learning Philosophical Transactions of the Royal Society 375, 20180406

Valeriani, D & Simonyan, K (2021) The dynamic connectome of speech control Philosophical Transactions of the Royal Society 376, 20200256

Vernes, S.C et al (2021a) Vocal learning in animals and humans Philosophical Transactions of the Royal Society 376, 20200234

Vernes, S.C et al (2021b) The multi-dimensional nature of vocal learning Philosophical Transactions of the Royal Society 376, 20200236

Wagner, H.O (1944) Notes on the life history of the emerald toucanet The Wilson Bulletin 56, 65-76

Wong, K (2019) Winged victory Scientific American November, 51-53

Zandberg, L et al (2021) Global cultural evolutionary model of humpback whale song Philosophical Transactions of the Royal Society 376, 20200242

6. PLAY

6.1. DEFINITIONS

Many different animals appear to play. But a definition of play is needed to avoid humans projecting their "playful nature" onto non-humans (Marshall 2021). Burghardt (2005) proposed five criteria based on various definitions:

i) The action should have no immediate purpose or goal - "the performance of the behaviour is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed toward stimuli, that do not contribute to current survival" (Burghardt 2005 quoted in Dapporto et al 2006).

ii) The behaviour is spontaneous, voluntary, intentional, and pleasurable (ie: "done for its own sake").

iii) The behaviour should be different from the functional equivalence (ie: a modified version of the actual behaviour) (eg: play fighting does not involve biting). For instance, among elephants placing the trunk on another's head is a sign of dominance, "but in calves is guaranteed to precipitate a spirited sparring match" (O'Connell 2021 p47).

iv) The behaviour is repeated - "the behaviour is performed repeatedly in a similar, but not rigidly stereotyped, form" (Burghardt 2005 quoted in Dapporto et al 2006).

v) The behaviour appears when the animal is relaxed, sated, and free from competition (eg: from predators or in relation to mating) (ie: in a "relaxed field"; Burghardt 2005).

Play can increase the versatility of movements when dealing with loss of balance and enhance the ability to cope with unexpected stressful situations. This can be done by "self-handicapping. For example, a lion cub deliberately gives some control over its body and allows littermates to pounce on it, then the roles are reversed. "Self-handicapping is risky and requires trust, but it is a great way to develop strength and agility. It is also an important exercise in building co-operation" (O'Connell 2021 p48).

In terms of unusual examples of play (or play-like behaviour), Dinets (2015) and crocodilians, and Dapporto et al (2006) among young adult female paper wasps.

6.2. CROCODILIANS

Responding to Burghardt's (2005) finding of only two published studies and three unpublished observations of apparent play in crocodilians, Dinets (2015) provided an overview from his work (over 3000 hours of observing wild and captive animals).

Seven play occurrences were noted. These were supplemented by informal data from people working with crocodilians at various conferences and via social media in 2013-14. In total, seventeen "records of possible play behaviour... but it is far more likely that these numbers reflect nothing more than observational coverage bias and the randomness of rare observation events" (Dinets 2015 p55).

Dinets (2015) concentrated on three types of play:

i) Locomotor play - Defined by Burghardt (2005) as "intense or sustained locomotor movements... often without any apparent immediate reason or stimulus" (quoted in Dinets 2015). Three potential observations were collected.

ii) Object play - This is the interaction with an object for pleasure (eg: floating large ball). Dinets (2015) stated: "Object play appears to be the most frequently observed type of crocodilian play; it is so common that many zoo caretakers now provide various objects as toys for crocodilians as part of habitat enrichment programmes" (p50).

iii) Social play - This is interaction between individuals, and is "almost never reported, but this doesn't mean that it is particularly rare" (Dinets 2015 p53).

Applying Burghardt's (2005) five criteria of play, Dinets (2015) was confident that the behaviour observed fulfilled them:

- Did not contribute to survival - eg: Dinets (2015) observed "a young adult American alligator in Saint Augustine Alligator Farm Zoo Park (Florida, USA) moving its head horizontally back and forth across a stream of water falling from a pipe and making snapping movements as if trying to bite the stream. This behaviour continued for over half an hour, sometimes interrupted with a few minutes of rest under the stream" (p50).

- Voluntary, repeated behaviour by relaxed individuals.

- Incomplete versions of actual behaviour - eg: Another case observed by Dinets (2015) in Florida was an interesting behaviour between an otter and an American alligator: "On one occasion an otter slipped on a steep bank of the bayou and was grabbed across the chest by the alligator. The alligator retreated from the bank and pulled the wriggling otter underwater as if attempting to drown it, but after about 5 s raised its head and released the otter, apparently unharmed. The interactions between this alligator and the otters then continued for two more days, at which point the bayou dried out and all otters and alligators moved elsewhere" (p54).

Dinets (2015) noted in conclusion that "energetic constraints reduce the probability of observing sustained vigorous behaviour typical of endothermic mammals and birds in ectothermic vertebrates. On the other hand, aquatic environment reduces the cost of locomotion, possibly facilitating the performance of play in crocodilians" (pp54-55). Though the aquatic environment made locomotor play less energy demanding.

6.3. PAPER WASPS

Dapporto et al (2006) admitted that the "idea that insects play has often aroused scepticism" (p394).

These researchers focused on the ritualised dominance behaviour (RDB) by young female Polistes dominulus paper wasps as a play-like behaviour. Twelve aggregations in five different locations in Italy over three years were observed. The wasps hibernate in aggregations before founding their own nests in the following six months. Dapporto et al (2006) described the RDB: "This behaviour consists of a sequence of patterns: The dominant female wasp approaches the subordinate, raising her head over the subordinate head, performing a rapid beating of the antennae, and often licking, biting, and asking for food. On the other hand, the subordinate lowers its body and, sometimes, offers regurgitated liquid droplets (trophallaxis [TRP]) to the dominant subject" (p394). This behaviour was performed in the aggregations with "exaggerated frequencies" six months before it would have been appropriate in a nest.

Dapporto et al (2006) assessed the RDB with Burghardt's (2005) five criteria of play (appendix 6A):

- Not fully functional.

- Voluntary and intentional - "If intentional (goal-directed) behaviours occur in wasps, a complex behaviour such as RDB is certainly one of these" (Dapporto et al 2006 p397).

- Different to actual behaviour.

- Repeated.

- Relaxed.

In summary, the RDB was analogous to "play fighting", though the researchers did not like this idea specifically. "By play fighting, immature animals assess their own strength, learn to cope with unpredictable situations..., and acquire social competence, thus attempting to establish dominance hierarchies well before any reproductive conflict could arise" (Dapporto et al 2006 p398). There is "phenomenological similarity" between play fighting and RDB (Dapporto et al 2006 p399).

6.4. APPENDIX 6A - STEREOTYPIC BEHAVIOURS

Captive animals can show abnormal behaviours not seen in the wild, like "stereotypies" (ie: "abnormal repetitive behaviours that involve the unvarying inappropriate repetition of a particular set of movements and/or body postures that lack any goal or function"; Fuktong et al 2021 p2). Stereotypies are taken as a sign of poor animal welfare. They can also be seen as the opposite to play with its voluntary and spontaneous characteristics.

Elephants kept in tourist camps (ie: employed to give rides) are a particular concern. For example, Varadharajan et al (2016) reported cases of stereotypic behaviours among 49 captive Asian elephants in Tamil Nadu, India, while Bansiddhi et al (2019) calculated a prevalence of a quarter of 84 elephants in camps in Chiang Mai, Thailand.

Building on this last study, Fuktong et al (2021) found a higher prevalence. Data were collected on 283 elephants in twenty tourist camps in Chiang Mai via direct observation, and questionnaires to 181 handlers (mahouts). Stereotypic behaviours was categorised if there were "unvarying, repeated behaviours that persisted for at least ten seconds or as three repetitions" (Fuktong et al 2021 p2).

From direct observations the prevalence of stereotypes was 57%, and 58% based on questionnaire responses [7]. There was some disagreement between observation and questionnaire data - seventeen elephants observed but not reported by handlers and 22 the opposite. These differences may be due to the limitations of 15-minute observation periods or the level of understanding of stereotypic behaviour by the handlers. Longer and/or video-recorded observation would be ideal.

The main behaviours were swaying (back and forth) (33% of elephants), weaving (swaying side to side) (17%), pacing (16%), bobbing (5%), limb movements (1%), and rocking (1%). Most elephants performed only one behaviour, but 3% of observed elephants performed three different types.

The study was able to cover one-third of all elephants in the tourist camps in Chiang Mai. It used direct observation as well as questionnaires, whereas Bansiddhi et al (2019) was based on handler questionnaires mostly. Fuktong et al (2021) noted that their study was "conducted when Thailand had closed its international borders because of the covid-19 pandemic and only local Thai tourists were visiting the camps, a reduction of 90-100% compared to pre-covid tourist numbers. Therefore, elephants experienced a reduction in work activities and an increase in social isolation" (p4).

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[7] Similar prevalence has been reported among elephants in UK zoos (Fuktong et al 2021).

6.5. REFERENCES

Bansiddhi, P et al (2019) Management factors affecting abnormal glucocorticoid activity of tourist camp elephants in Thailand and implications for elephant welfare PLoS ONE 14, e0221537 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0221537)

Burghardt, G (2005) The Genesis of Animal Play: Testing the Limits Cambridge, MA: MIT Press

Dapporto, L et al (2006) Dominance interactions in young adult paper wasp (Polistes dominulus) foundresses: A play-like behaviour? Journal of Comparative Psychology 120, 4, 394-400

Dinets, V (2015) Play behaviour in crocodilians Animal Behaviour and Cognition 2, 1, 49-55

Fuktong, S et al (2021) A survey of stereotypic behaviours in tourist camp elephants in Chiang Mai, Thailand Applied Animal Behaviour Science 243, 105456

Marshall, M (2021) When geckos play basketball New Scientist 18th/25th December, 77-78

O'Connell, C (2021) Why animals play Scientific American August, 44-50

Varadharajan, V et al (2016) Prevalence of stereotypies and its possible causes among captive Asian elephants (Elephas maximus) in Tamil Nadu, India Applied Animal Behaviour Science 174, 137-146

7. PREDATION AND DEFENCE

7.1. PREDATION

Around half, on average, of an animal's lifetime activity budget involves finding food (Fulgence et al 2021). Predation is one way to find food, and this includes vertebrates preying on other vertebrates [8], and vertebrates preying on invertebrates. But invertebrates preying on vertebrates is rare (Fulgence et al 2021).

In a review, Valdez (2020) collated examples including crabs preying on frogs, and water bugs preying on fish (appendix 7A). Fulgence et al (2021) concentrated on a spider trapping a frog, specifically a spider from the genus Damastes and a frog Heterixalus andrakata) in Madagascar.

Four chance (or incidental) observations were made during other research in 2017 and 2018. The spider wove leaves together with spider silk in order to have a place to hide (a retreat) and to wait for a passing frog to seek cover within.

The spider genus is part of a group called "huntsman spiders", who do not buold webs, but either actively hunt for prey or sit-and-wait as in this case (Fulgence et al 2021).

Other spiders that prey on vertebrates do so either by active hunting, or by catching them in mid-air with webs (eg: birds) (Fulgence et al 2021).

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[8] For example, it is estimated that arthropod predators consume 400-800 million metric tons of insect prey globally annually (Valdez 2020).

7.1.1. Diversity

"Diversity in hunting patterns and behaviour allows predators to exploit new food resources, expand their range of potential prey items, improve their odds of successful prey capture and limit competition" (Tietbohl et al 2020 p1569).

On coral reefs, triggerfishes show such diversity. For example, suction feeding for small and soft-bodied prey, but biting of harder and larger prey, and water-jetting (forcibly ejecting water from the mouth while closing the gill opening) to uncover invertebrates hidden in the sand (Tietbohl et al 2020).

Tietbohl et al (2020) reported a novel hunting strategy of the titan triggerfish (Balistoides viridescens) (figure 7.1) - namely, intentional partial beaching of itself. In May 2018 on Mar Mar island in the Red Sea, a ghost crab was seen foraging on algae along the shoreline, when a triggerfish made several partial-beaching attempts before successfully capturing the prey. This strategy "minimises potential competition from other marine invertivores while simultaneously exploiting a food resource inaccessible to most coral reff fishes" (Tietbohl et al 2020 p1571). This could be evidence of social learning.

(Source: Jan Derk; in public domain)

Figure 7.1 - Titan triggerfish.

Other species of triggerfish have been observed in the Red Sea showing novel feeding behaviour (eg: pick up urchins, carry them upwards, drop them from a height in the water, and feed on exposed underside as they fell) (Tietbohl et al 2020).

Not only is the behaviour uncommon for marine fish, but a fish feeding on terrestrial prey is unsual (Tietbohl et al 2020). Cucherousset et al (2012) reported a catfish beaching while feeding on pigeons in France, for instance (figure 7.2).

(Source: Cucherousset et al 2012 figure 1)

Figure 7.2 - A catfish beaching itself to catch pigeons drinking by the river's edge.

7.2. ANTI-PREDATOR STRATEGY

Prey cornered by a predator can respond by signalling their toxicity (conspicuous colouration), startling the predator in some way (eg: sudden flash of colour), or by diverting the attack to expendable body parts ("deflection"), for instance.

Heathcote et al (2020) described "a new type of divertive anti-predator strategy" used by Trinidadian guppies (Poecilia reticulata). The guppies used "conspicuous colouration to direct attacks to a predictable location on their body and, once the predator has committed to its attack, the prey uses a 'matador-like' strategy whereby they execute a split-second escape response that takes them safely out of the predator's diverted attack path" (Heathcote et al 2020 pp2844-2845). This seems counter-intuitive because the prey is encouraging interaction with the predator.

Pike cichlids (Crenicichia alta) are ambush hunters of guppies, and the "guppies frequently approach and inspect detected predators to determine their predatory motivation" (Heathcote et al 2020 p2845). Heathcote et al (2020) observed this behaviour with models of the predator. As the guppies approached, they blackened their irises which made them more conspicuous.

The researchers proposed two hypotheses to test: "(1) attack deterrence: black-eyed guppies deter predators, such as via pursuit deterrent signalling or by increasing their perceived size; or (2) attack diversion: conspicuous eyes divert predator attacks to the guppy's head, which enhances evasion when combined with the guppies' rapidly pivoting escape response" (Heathcote et al 2020 p2846). The tests involved 52 wild pike cichlids caught in a mountain river in Trinidad. Model guppies were constructed with different eye colouration (black or silver).

Both eye colour-models were attacked equally (36% for black eyes and 33% silver eyes), which was taken as lack of support for the deterrence hypothesis. the area of the model attacked by the predator was recorded. The silver-eyed models were attacked at their centre, whereas the black-eyed ones at their head. This supported the attack diversion hypothesis. But "all the attacked robots were still engulfed by the cichlids, suggesting that rather than benefiting from deflection, the divertive effect must work in concert with the prey's escape response to be adaptive" (Heathcote et al 2020 p2847).

This was tested by putting live guppies and live pike cichlids together, but separated by a transparent barrier. Black-eyed and silver-eyed guppies were used. "Guppies displaying black irises that anteriorly diverted a predator's attack increased their escape probability by an average of 38.8% compared to silver-eyed fish that were attacked at their centre of mass..." (Heathcote et al 2020 p2847). Larger guppies benefited more from this strategy.

This "matador-like" strategy works because "once their lunge has been initiated, cichlids do not alter their attack path in relation to the guppy's resultant escape trajectory..." (Heathcote et al 2020 p2847).

7.3. CATFISH

The African electric catfish (Malapterurus beniensis) is able to generate powerful electric shocks "emitted by a specialised electric organ which is composed of a thin layer of electrocytes located directly below the skin that covers nearly the whole body" (Welzel and Schuster 2021 p1). The electric shock is used in prey capture (to immobilise), and defence, as well as possibly in communication and social interactions with conspecifics (Welzel and Schuster 2021).

"High-voltage electric shocks have massive effects on the nervous system... as well as the skeletal muscles of fish" (Welzel and Schuster 2021 p1). Welzel and Schuster (2021) investigated this impact as to whether electric catfish are self-protected against their shocks. Two electric catfish were tested experimentally.

The catfish was stimulated to produce an electric discharge with a sudden auditory pulse (self-produced) and including the other catfish, and shocked externally with electro-fishing equipment. Two electrodes were placed in the water and an electric current passed between them as the fish swam through. Five goldfishes were used as controls.

The catfish did not twitch in response to their own defensive electric discharge nor the discharge of another catfish, and the electro-fishing shock. The goldfishes were immobilised briefly by the electro-fishing equipment.

Overall, there was no involuntary muscle twitch to the different electric shocks which suggested that "electric catfish are completely immune not only to their own high-voltage electrical shocks but also to external shocks delivered by a commercial electro-fishing device" (Welzel and Schuster 2021 p7).

Welzel and Schuster (2021) stated that "the easiest explanation of our findings is probably that electric catfish achieve immunity by highly resistive tissues that shield the whole animal or, individually, its muscles, heart and nervous system. Alternatively, or perhaps additionally, some tissues might have evolved some intrinsic tolerance" (p8).

The researchers video-recorded the experiments and so analysed the behaviour of the catfish very carefully. This allowed them to dismiss the explanation that "the discharging catfish prepares for the effects of its electric shocks, similar to how an echolocating bat prepares before emitting a potentially deafening high-intensity echolocation call...: electric catfish are equally well protected against external discharges whose timing and waveform they cannot control" (Welzel and Schuster 2021 p8).

7.4. CHIMPANZEES

Intra-species violence involves members of the same species, while inter-species violence is between members of different species (not necessarily related to predator-prey interactions). The former has been observed among chimpanzees, and among gorillas, but Southern et al (2021) reported potentially the first case of chimpanzees attacking and killing gorillas.

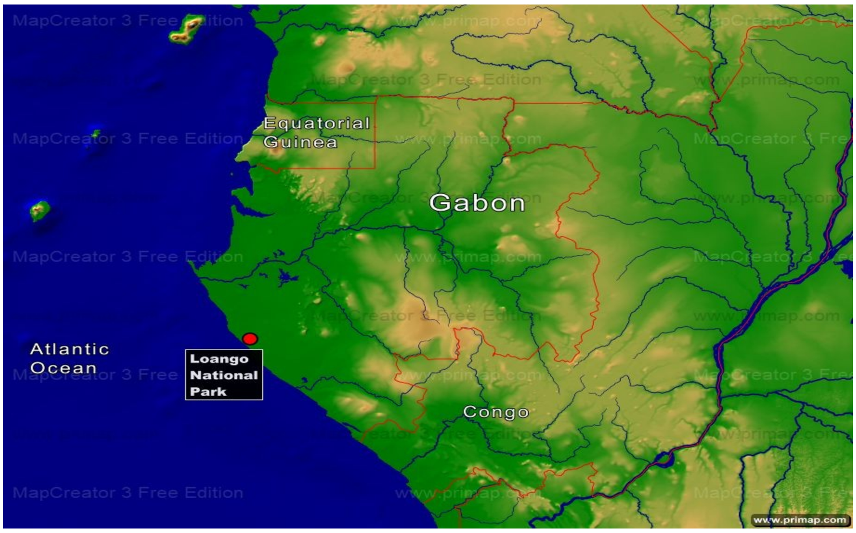
Two lethal encounters were observed by the researchers in Loango National Park, Gabon (figure 7.3), where a community of forty-five chimpanzees has been observed for a number of years. In the first case, on 6th February 2019, eighteen chimpanzees encountered five gorillas, and it resulted in one dead gorilla infant and three injured chimpabzees. The second encounter (27 chimpanzees and seven gorillas) resulted in one dead gorilla infant on 11th December 2019.

Southern et al (2021) considered two possible explanations for the behaviour:

a) Opportunistic predation by the chimpanzees - There was some consumption of the dead gorilla in the second case, but "the behaviours observed during the two events were very different to those reported during hunting..." (Southern et al 2021 p6).

b) Inter-species competition over resources.

The researchers preferred the latter explanation as chimpanzees are known to kill resource competitors from



(My drawing using MapCreator3)

Figure 7.3 - Position of Loango National Park.

their own and other species. "The two lethal encounters we observed occurred at times characterised by food scarcity and a period of high dietary overlap (for fruit resources) — February and December 2019. In contrast, the two previously observed peaceful co-feeding events took place in April, a month characterised by relatively low dietary overlap between the two species" (Southern et al 2021 p6).

Many observations are needed before a fuller picture of such behaviour can be established, particularly as to whether it is typical of chimpanzees or specific to particular situations.

7.5. ANTS

Ants can adapt to species, resources or environmental conditions. This means that there will be unusual behaviours between species. One such is the ant species Pheidole oxyops [9] that deliberately places bird feathers around the entrance to the ground nest (Gomes et al 2019).

The nest has "a peculiar structure, with a wide,

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[9] General information about this species at https://www.antweb.org/description.do?genus=pheidole&species=oxyops&rank=species&museumCode=MCZC.

deep, and smooth entrance tunnel, which is thought to work as a pitfall trap, enhancing the capture of arthropod prey... Feathers may thus further enhance prey capture, given that they may work as bait (due to their smell, colour or shape) to some arthropods that end up falling into the nest entrance tunnel. In addition, it is possible that feathers directly benefit ants, as they could obtain food from small residues of bird tissue or from prey present in the feathers" (Gomes et al 2019 pp451-452). Alternatively, the feathers may act as moisture retainers and supply the colony with water in the dry Brazilian savannas where these ants live (Gomes et al 2019).

Gomes et al (2019) tested the two possibilities - feathers to aid prey capture, or as moisture retainers. In relation to the former explanation, the researchers built pitfall traps (similar to the ants' nest entrance) with feathers around them (n = 10) and without (n =10) in the university grounds in Brazil. Gomes et al (2019) explained: "After 48 h, we collected the pitfall traps and took them to the laboratory, where the arthropods were sorted into morphospecies. If feathers do enhance prey capture, we expected that traps with feathers would collect more arthropod species and individuals than would traps with no feathers" (p452). Significantly more arthropods were found in the feather-traps than the controls, even after removing non-food species for the ants.

To test the hypothesis about feathers and water, during the dry season the researchers removed the feathers from around twenty-eight nests in Minas Gerais, Brazil. Half the nest had water-soaked cotton balls left instead ("water-addition group"), and half nothing ("no-water group"). After three days a handful feathers were left near the nests. Gomes et al (2019) outlined their expectations: "If feathers act as a water source for ants, we expected that the no-water group would collect more feathers than the water-addition group" (p453). There was no difference in the number of feathers collected between the two groups. Gomes et al (2019) admitted that "this experiment was conducted over a short period of time; it is possible that three days were not enough to produce significant changes in water availability to the nest" (p455).

Overall, this research supported the idea that these ants used the feathers to enhance a passive strategy of prey capture (ie: "sit and wait" for prey). But Pheidole oxyops also actively seek prey away from the nest (Gomes et al 2019). The arthropods caught in the pitfall traps suggested an increase in diet diversity compared to active prey seeking (Gomes et al 2019).

Ants using traps is rare, but it has been observed in the plant-ant Allomerus decemarticulatus, who construct a gooey platform on the plant they inhabit to capture large insects that land there (Dejean et al 2005).

Gomes et al (2019) did not test other hypotheses for the feathers including as camouflage of the nest entrance against predators, or as protection against potential flooding of the nest in the wet season.

7.5.1. Ants vs Spiders

"At the population level, there is a negative correlation between the density of ant populations and the total biomass of spiders" (Fischer et al 2021 p2). In other words, ants and spiders tended not to be found in large numbers in the same places.

Fischer et al (2021) studied this relationship specifically with three ant species and four web-building spider species (table 7.1).

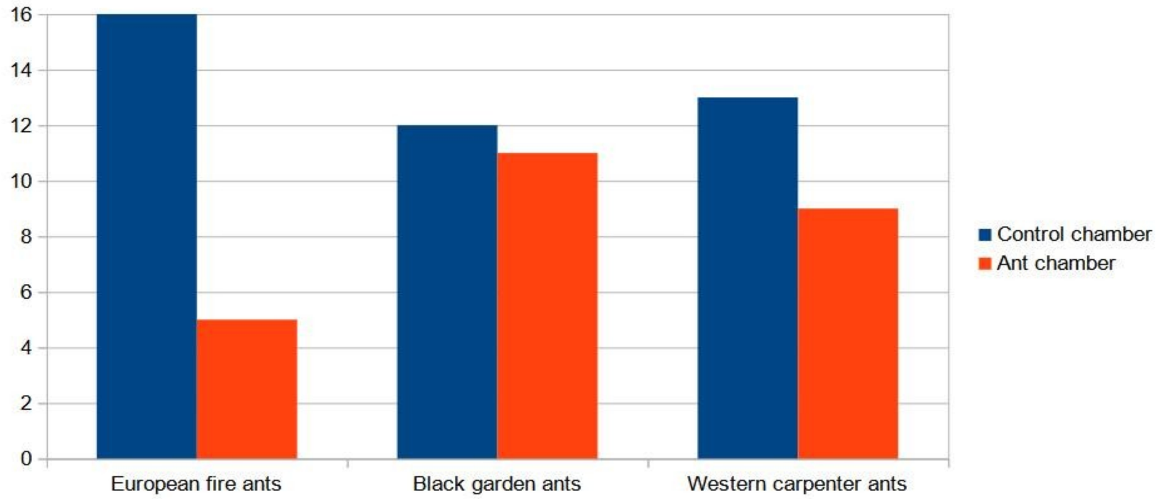
- European fire ant (Myrmica rubra)
- Black garden ant (Lasius niger)
- Western carpenter ant (Camponotus modoc)

- False black widow spider (Steatoda grossa)
- Western black widow spider (Latrodectus hesperus)
- Cross spider (Araneus diadematus)
- Hobo spider (Eratigena agrestis)

Table 7.1 - Species used in experiments.

In the experiments, 75 workers of each ant species were used, and the spiders were female sub-adults, all captured around Canada. An individual spider was presented with a choice of two chambers, one of which had housed the ants for twelve hours previously (ie: infused with chemical signals; semio-chemicals), and the other was the control. The spider was left in darkness for 24 hours, and their place of web-building was filmed. Ten versions of the experiment were performed with different ant and spider species, and the control chamber was varied to overcome any lateral preference.

The chemical scent of the European fire ants had a significant deterrent effect on all four species of spider (ie: preference for the control chamber). There was no effect with the other two ant species (figure 7.4).



(After Fischer et al 2021 figure 2)

Figure 7.4 - Number of false black widow spiders choosing different chambers based on species of ant.

The researchers considered an explanation for the findings. One possibility was that fire ants are aggressive and could attack the spiders who live in the same habitat. "It is conceivable then, that over evolutionary time arthropod community members, including spiders which may fall prey to M. rubra, have learned to respond to semio-chemical cues of M. rubra and to settle in (micro) habitats void of M. rubra" (Fischer et al 2021 p6).

Alternatively, there may have been methodological issues with the experiments. For example, the experimenters had no objective way of standardising the chemical cues, and so it was assumed, as a rule of thumb, that larger ants deposit greater amounts. But this may not have been so. Also it is not known if the chemicals are excreted by glands or the body surface of the ants (Fischer et al 2021).

7.6. HARES AND COAT COLOUR MISMATCH

Climate change can impact species through "phenological mismatch". This is where a seasonal behaviour becomes unsynchronised with the earlier onset of spring or the delayed onset of winter. One obvious example of this is the changing of coat or plumage colour to fit with the environment (eg: snow and non-snow). Over twenty bird and mammal species in the Northern Hemisphere have seasonal biannual changes as camouflage (Kennah et al 2021).

The reduction in snow cover duration with global warming will lead these animals to a colour mismatch (ie: a white coat in a non-snow environment). This will increase the risk of predation.

Kennah et al (2021) concentrated on the snowshoe hare (Lepus americanus) in North America that has a colour change to a white coat (from brown) triggered by lessening daylight. Increased predation has been reported in recent years (eg: Wilson et al 2018). "However, the thermal benefits of winter acclimatisation in hares, including reduced metabolic rate..., may also affect susceptibility to predation and ultimately survival" (Kennah et al 2021 p5). White winter-acclimatised hares appear to require less food at lower temperatures than brown summer-acclimatised hares, and so forage less with reduced exposure to predators (Kennah et al 2021).

Data were analysed from three autumns (2015-2017) and four springs (2015-2018) in southwestern Yukon, Canada, where hares have been observed for over forty years (Kennah et al 2021).

Tagged individuals were categorised as matched (autumn/white coat or spring/brown coat) or mismatched (autumn/brown coat or spring/white coat). Daily time spent foraging was calculated for each hare.

In total, 347 hares were monitored, of which forty-one died in the springs and 34 in the autumns.

The average daily foraging time was 706 minutes in the spring and 751 minutes in the autumn. Coat colour mismatch predicted daily foraging time only in the autumn. As the temperature dropped in autumn, mismatched hares foraged for less time compared to matched hares (eg: at -8°C the difference was 65 minutes per day).

Overall, mismatched hares had a survival rate in the autumn, but there was no difference compared to matched hares in the spring. This is contrary to previous studies. Kennah et al (2021) offered this explanation: "Mismatched white hares spent significantly less time foraging than matched individuals in the autumn, presumably due to the thermal and energetic benefits of winter acclimatisation. Indeed, reduced foraging time likely decreases exposure to predators and subsequently improves survival" (p15). So, white coats not only provided a benefit of camouflage in the snow, but they are warmer (thus the need for less food).

The previous studies were further south (eg: Wilson et al 2018: Wisconsin, USA), where the temperatures are warmer (Kennah et al 2021).

7.7. VIPER HORNS

Convergence in evolution is where the same traits have evolved independently in different species or animals. "If a trait evolved independently and is associated with a similar environment or ecological niche, it is likely to be adaptive to that environment" (Busschau and Boissinot 2022 p652).

Horn-like appendages among reptiles is an interesting example. In horned lizards, say, cranial horns evolved for defence against predators, while among chameleons, "horns are used in male combat, territorial displays, or to persuade females during copulation and are thus under strong sexual selection" (Busschau and Boissinot 2022 p652).

Busschau and Boissinot (2022) considered horns among over two hundred viper (Viperidae) species. The researchers found a relationship between habitat and the relative position of the horns on the head area. Nasal horns (ie: on the nose area) (figure 7.5) in a species was associated with living in terrestrial forest habitats, ocular horns (ie: above the eye area) (figure 7.6) in a species was associated with a sparsely vegetated habitat.

Busschau and Boissinot (2022) explained: "Terrestrial forest habitats are typically covered in a layer of leaf litter or foliage which terrestrial vipers utilise as concealment to ambush prey. Here, nasal horns could potentially disrupt the outline of a viper's head or resemble the substrate, making it more difficult to detect against a background of leaves and twigs" (p660). While ocular horns "could contribute significantly to concealing the eyes and disrupting a viper's silhouette in more exposed ambush sites" (Busschau and Boissinot 2022 p661). It is suggested that the different horns evolved independently in the different species because of similar selection pressures of the environment. This is the convergent evolution of horns in vipers.

(Source: Mircea Nita; in public domain)

Figure 7.5 - Example of nasal horns - Horned viper.

(Source: Victorrocha)

Figure 7.6 - Example of ocular horns - sidewinder.

7.8. ACOUSTIC CRYPSIS

Eggs are vulnerable to predators, particularly those of ground-nesting species. Visual crypsis of the eggs acts as a camouflage for them (ie: the colour of the eggs match the surrounding environment). But embryonic calling, which occurs in the late stage of incubation, compromises visual crypsis.

So, embryonic calling needs to cease if predators are nearby, which requires the embryo to respond to predator calls or parental alarm calls. This "acoustic crypsis" requires pre-natal acoustic discrimination and vocal learning (known as the "predator information hypothesis") (Kostoglou et al 2021).

The ability to listen and learn while in the egg has been found in a small number of bird species (eg: domestic chicken) (Kostoglou et al 2021).

Alternatively, the embryo may respond to parental heart rate communicated via brood patches. These, "which thermally couple incubating adults with eggs, are highly vascularised... and avian heart rates are audible from within the egg... When under stress (ie: when predators are nearby or approaching), parental heart rate can drastically increase" (Kostoglou et al 2021 p1426). This is the "physiological cues hypothesis".

A third possibility is the "parental absence hypothesis". At the appearance of a predator, the parents leave the nest in order to draw the attacker away from the eggs. The embryo is able to sense this via change in light levels, temperature, and the general acoustic environment.

Kostoglou et al (2021) tested these three hypotheses in experiments with Red-capped plover (Charadrius ruficapillus) and Masked Lapwing (Vanellus miles) eggs.

In each experiment, an egg close to hatching was placed in a light-proof sound-insulated container and the embryo's calls were recorded (for three minutes). The experiments were:

1 - Three minutes of calls - either predator bird, parental alarm, benign local bird, or white noise (control).

2 - Exposure to recording of slow heart rate, fast heart rate, or silence for three minutes.

3 - Light, temperature and ambient noise were varied by taking the lid off the container.

In total 58 Plover eggs and 299 Lapwing eggs from nests in the Cheetham Wetlands, Point Cook, Victoria, Australia in 2017-18 and 2018-19 were involved.

In experiment 1 only predator calls produced significantly fewer embryonic calls compared to white noise. Experiments 2 and 3 found no significant differences. These findings supported the "predator information hypothesis". "Embryos appear to exhibit anti-predator crypsis even before they hatch, demonstrating an apparent ability to discern predator calls from the surroundings and to change their behaviour..." (Kostoglou et al 2021 p1429).

There was one problem for the researchers. "Contrary to our predator information hypothesis, embryonic calling rate for both species did not change in response to parental alarm calling when compared with the control (white noise). Perhaps parental alarm calls, at least for Red-capped Plovers and Masked Lapwings, that can occur while on or near the nest, are an unreliable indicator of predator presence in the sense that the same alarm call may be used for other threats, eg: during territorial disputes, which do not pose a risk to eggs and/or chicks" (Kostoglou et al 2021 p1431).

The experimenters could not rule out the combination of different modes (eg: calls, heart rate, and light changes) to communicate threats to embryos. Kostoglou et al (2021) admitted: "Anti-predator behaviour is a multi-modal response, where possible costs and benefits associated with a particular response are great. Adults, and conceivably embryos, may rely on a range of environmental, physical and acoustic cues to decide on a suitable anti-predator behaviour. We acknowledge that we tested some, but not all, possible cues available to embryos to judge external predator risk and that a greater sample size for Plovers would help confirm the ambiguous effect of different predator calls. The role of vibrations, emanating from parents and other eggs, constitutes another possible signal which may mediate anti-predator responses" (Kostoglou et al 2021 p1432).

Pre-natal sound may be involved in developmental programming in birds (ie: that it affects physiological development of the egg). Udino et al (2021) investigated the pre-natal exposure to "heat-calls" by zebra finches given during high environmental temperatures and the impact upon mitochondrial metabolism. The upshot is smaller nestlings in hot nests. The heat-calls during incubation aid the thermoregulation of the caller.

In a laboratory in Australia the researchers varied the temperature of nest boxes (25 °C (room temperature), 35, 40, 42 and 44 °C), and the playback of heat-calls.

Heat impacted development, but heat-calls improved the efficiency of the mitochondrial metabolism. In summary, "pre-natal sound alone is capable of reprogramming mitochondrial function" (Udino et al 2021 p7).

7.9. APPENDIX 7A - VALDEZ (2020)

Valdez (2020) performed a literature review using key search terms like "arthropod", "spider", "insect", "vertebrate", and "prey". Only observed cases in natural (not laboratory) settings were included.

A total of 1309 arthropod predation events on vertebrates were found in 737 references (published between 1965 and 2020).

Nearly half of all cases were arachnids, who were the main predators for all vertebrates preyed upon except birds. This is not surprising for a number of reasons (Valdez 2020):

a) The large number of spiders in the world (an estimated global biomass of 25 million metric tons; Valdez 2020).

b) Spiders are the subject of many studies.

c) Spiders "possess strong fangs capable of piercing vertebrate skin and injecting them with neurotoxins, many specific to the nervous system of vertebrates" (Valdez 2020 p1698).

d) Spiders "have a diversity of tactics such as active hunting, sit-and-wait ambush, and for many, the production of webs that can entangle many small animals. These webs are so strong that birds are often found entangled in them..." (Valdez 2020 p1698).

e) Spiders grow larger than most arthropods.

Generally, wandering spiders (nocturnal, venomous, ambush hunters) prey mostly on frogs, while tangle-web spiders (web-builders, venomous) prey on lizards and rodents, nursery web spiders (eg: fishing spiders) on amphibians and fish, and orb-weaver spiders (strong and large webs) birds and bats.

Valdez (2020) made this comment: "Spiders that build webs are generally more conspicuous and visible to humans, who will notice and recognise the captured prey, especially since prey items typically remain stuck in the web for a period of time. Observers will remember where they saw webs and may therefore consciously or subconsciously look for other prey items within these webs. This contrasts with non-web weaving spiders, in which an observer must be in the right place at the right time to be lucky enough to see a predation event" (p1698).

He continued: "Caution is advised when interpreting these results since the frequency or patterns recorded in the literature may not be representative of what occurs in nature, especially since some arthropod predators and predatory events may be more cryptic and much harder to observe than others, making such interactions under-represented" (Valdez 2020 p1699).

7.10. REFERENCES

Busschau, T & Boissinot, S (2022) Habitat determines convergent evolution of cephalic horns in vipers Biological Journal of the Linnean Society 135, 4, 652-664

Cucherousset, J et al (2012) "Freshwater killer whales": Beaching behaviour of an alien fish to hunt land birds PloS ONE 7, 12, e50840 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0050840)

Dejean, A et al (2005) Insect behaviour: Arboreal ants build traps to capture prey Nature 434, p973

Fischer, A et al (2021) Know your foe: Synanthropic spiders are deterred by semio-chemicals of European fire ants Royal Society Open Science 8, 210279

Fulgence, T.R et al (2021) Spider traps amphibian in northeastern Madagascar Ecology and Evolution 11, 682-687

Gomes, I.J.M.T et al (2019) Why do Pheidole oxyops (Forel 1908) ants place feathers about their nests? Ecological Entomology 44, 4, 451-456

Heathcote, R.J.P et al (2020) A matador-like predator diversion strategy driven by conspicuous colouration in guppies Current Biology 30, 2844-2851

Kennah, J.L et al (2021) Coat colour mismatch improves survival of a keystone boreal herbivore: Energetic advantages exceed lost camouflage bioRxiv (https://www.biorxiv.org/content/10.1101/2021.09.24.461654v1)

Kostoglou, K.N et al (2021) Shorebird embryos exhibit anti-predator responses Ibis 163, 1425-1436

Southern, L.M et al (2021) Lethal coalitionary attacks of chimpanzees (Pan troglodytes troglodytes) on gorillas (Gorilla gorilla gorilla) in the wild Scientific Reports 11, 14673

Tietbohl, M.D et al (2020) Intentional partial beaching in a coral reef fish: A newly recorded hunting behaviour of titan triggerfish, Balistoides viridescens Journal of Fish Biology 97, 1569-1572

Udino, E et al (2021) Pre-natal acoustic programming of mitochondrial function for high temperatures in an arid-adapted bird Proceedings of the Royal Society B 288, 20211893

Valdez, J.W (2020) Arthropods as vertebrate predators: A review of global patterns Global Ecology and Biogeography 29, 10, 1691-1703

Welzel, G & Schuster, S (2021) Efficient high-voltage protection in the electric catfish Journal of Experimental Biology 224, jeb239855

Wilson, E.C et al (2018) An experimental translocation identifies habitat features that buffer camouflage mismatch in snowshoe hares Conservation Letters 12, 1-8