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More Behaviour of Animals

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

A complete listing of his writings at http://psychologywritings.synthasite.com/. See also material at https://archive.org/details/orsett-psych.

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1. DOMINANCE HIERARCHIES AFTER A CENTURY

1.1. HISTORY AND TERMS

Hobson (2022) made this general observation: "Competition is nearly ubiquitous in situations where resources are limited and contested. Because of this, conflict is inevitable in most social groups, leading to increased access to these resources for some individuals and decreased access for others. In many social species, this competition leads to the emergence of group dominance hierarchies, which can help make social life more structured and predictable and regulate overall conflict" (p1).

Thorlief Schjelderup-Ebbe (1922) coined the term "pecking order" ("Hackliste" in the original German) around a century ago to describe the behaviour of chickens. Based on many years of observations of domestic chickens from childhood, it was clear that hens pecked each other during feeding competition. But "certain hens were the 'despots', able to peck all others, whereas other hens were pecked by all others" (Strauss et al 2022a p1). This was the beginning of research on "dominance hierarchies".

Strauss et al (2022a) introduced a special issue of the journal "Philosophical Transactions of the Royal Society B" to mark one hundred years since Schjelderup-Ebbe's publication with a consideration of the state of knowledge. Firstly, that which is known with confidence:

i) Dominance hierarchies are found in many species.

ii) Dominance is a product of social relationships. Drew (1993) defined dominance specifically as "an attribute of the pattern of repeated, agonistic interactions between two individuals, characterised by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation" (quoted in Strauss et al 2022a).

iii) There is variability in the structure of dominance hierarchies between different species (eg: "egalitarian" or "despotic").

iv) "Position in the dominance hierarchy is determined by a combination of attributes of individuals, stochastic processes, and social context" (Strauss et al 2022a p3).

v) The position in the dominance hierarchy mostly associates with fitness-related outcomes (eg: high dominance and increased reproductive success).

If these points above are the "answered questions", there are still unanswered ones and unresolved issues, like (Strauss et al 2022a):

a) Defining dominance with more precision.

b) Understanding more about the physiology and neurobiology of dominance.

c) Variations in the structure of dominance hierarchies and individual behaviours.

d) The emergence of dominance hierarchies and how they change over time.

Over one hundred years there has been much research on dominance hierarchies, but the focus of the research has changed with time. Hobson (2022) concentrated on the latter in her survey of studies on the topic on "Google Scholar" (over 22 000). Simply, the number of publications on the topic increased with time, with a peak in the early 21st century.

So, "dominance research has had substantial interest over its long history", but have researchers "'solved' dominance" (Hobson 2022 p7)? Hobson (2022) answered (wryly): "Informally, and depending on who you talk to at conferences, the question of dominance has been 'solved' in the 1960s, the 1970s, the 1980s, or the 2000s" (p7).

But the focus of research has changed - for example, genetic and computational methods have grown in importance in recent years - and "new, more complex ways of studying the decisions animals make about who, when, and how they fight each other, and the consequences of different conflict management styles, provide a strong foundation for the next 100 years of dominance hierarchy research" (Hobson 2022 p7).

Hobson's (2022) analysis of the publication trends and terms used (ie: the publication metadata) rather than the research itself has been called "the science of science perspective" (p7).

Strauss et al (2022b) described an open archive ("DomArchive") containing datasets on over 243 000 agonistic interactions in 135 species from the last one hundred years. The data came from 190 studies. The researchers expressed the hope that the archive "will serve as an important resource for future comparative studies and will promote the development of general unifying theories of dominance in behavioural ecology that can be grounded in testing with empirical data" (Strauss et al 2022b p1).

1.2. BASIS OF DOMINANCE

Lewis (2022) pointed out that "[A]lmost since its inception, the study of dominance has been plagued by inconsistency. As researchers endeavoured to detect the phenomenon in other taxa, the problem of how to operationalise a pecking order for species that do not peck was solved using conflicting criteria" (p1). These criteria included biological traits (like body colouring), or individual actions (eg: aggression), while other studies viewed dominance as "a theoretical construct or an intervening variable rather than a way to arrange individuals in an orderly fashion" (Lewis 2022 pp1-2).

So, how to classify dominance in the dominance hierarchy? One answer is the "power framework" (eg: Lewis 2002), which combines different criteria. Power is defined as "a phenomenon emerging from an asymmetry in a dyadic relationship that results in one individual being able to influence the other" (Lewis 2022 p2). Four dimensions of power are distinguished (Lewis 2022):

i) Base (strength) - eg: fighting ability; knowledge.

ii) Means (aggression) - eg: aggressive behaviour; persuasion.

iii) Scope (winning) - eg: priority of access; submission.

iv) Amount (context) - eg: location in territory.

This approach moves away from dominance as only based on aggression to power through knowledge and persuasion (sometimes called a "leverage hierarchy") (Lewis 2022).

Many of Schelderup-Ebbe's (1922) original observation are still relevant, including (Lewis 2022):

a) An individual can occupy a low position in one group's hierarchy, but a high position in another group (ie: context).

b) Individuals behave differently when they first meet as to when a relationship has been established.

c) Broody, tired or hungry hens behaved differently to their usual behaviour (ie: context).

d) Past wins and losses are relevant. Eg: "After losing, an individual may seek conflict in a relationship with a different partner with less power in order to blunt some of the costs of losing (ie: redirected aggression)" (Lewis 2022 p4).

But position in the pecking order does not guarantee winning in a conflict.

Lewis (2022) summed up: "A focus on strength, aggression and fighting provides an incomplete understanding of the power landscape that individuals actually experience. Multiple methods for constructing hierarchies exist but greater attention to the implications of the types of data used in these constructions is needed. Many shifts in our understanding of power were foreshadowed in Schjelderup-Ebbe's discussion about deviations from the linear hierarchy in chickens" (p1).

1.3. CHANGE IN RANK

Individuals can move up and down the dominance hierarchy. Wallace et al (2022) studied experimentally the social ascent of male Burton's mouthbrooder cichlid

(Astatotilapia burtoni) [1]. Dominant males are colourful, and territorial, while subordinates are drab, and reproductively repressed.

Stable dominance hierarchies were allowed to form, and then the four largest males (ie: the most dominant individuals) were removed. Ten remaining males ascended and seventeen did not.

The changes in the ascenders were studied with tests before and after the removal of the dominant individuals. For example, in the novel object recognition test, which measures a preference for familiar or novel objects, the ascenders preferred the familiar object before, but the novel object after removal of the dominants. This may reflect territorial behaviour, which is a characteristic of reproductively dominant individuals. Non-ascenders did not change their behaviour in this test. Changes in hormone levels were also found in ascenders.

Wallace et al (2022) ended: "Social ascent elicits a dramatic suite of changes across biological levels" (p11).

The alternative is "dominance certainty" (or "rank stability") - "the likelihood an individual's rank might remain stable, ie: unchanged through time, on account of the consistency in the outcome (wins and/or losses) of its agonistic encounters with its conspecifics" (McCowan et al 2022 p2). Studies of captive rhesus monkeys, for instance, suggest that "the certainty (or predictability) about one's position in the network of status relationships may be just as important as absolute rank in predicting health outcomes" (McCowan et al 2022 p5).

1.4. LEVEL OF AGGRESSION

Dominance interactions involve obvious costs like substantial injury, depletion of energy, time when not foraging, and less vigilance of predators. "Accordingly, to maximise the net benefits of investing in dominance interactions, individuals should be strategic in terms of whom they direct their interactions towards, such that they may attain or maintain their position in the hierarchy at minimal cost to themselves" (Dehnen et al 2022 pp1-2).

The best strategy is that "aggressive interactions should be directed towards competitors closer in the hierarchy, as the directionality of the dominance relationship is likely to be less well established, and

[1] Information at https://www.fishbase.se/summary/Astatotilapia-burtoni.html.

most vulnerable to change, between closely matched competitors" (Dehnen et al 2022 p2). While less aggression should be directed at clearly lower ranked individuals. This "strategic aggression" has been observed in gorillas, monk parakeets, and feral dogs, for example (Dehnen et al 2022).

But alternatives have also been reported - "bullying" (more aggression towards lower than equally ranked individuals) or "downwards heuristic" (equal levels of aggression to all individuals) (Dehnen et al 2022).

Dehnen et al (2022) investigated these different ideas with vulturine guineafowl (Acryllium vulturinum) (figure 1.1) in Kenya. There were two groups containing 23 and 29 males respectively. Over 7300 male-male dominance interactions were observed between 2019 and 2021. Interactions were categorised into "higher-cost

(Source: Xcolati; in public domain)

Figure 1.1 - Vulturine guineafowl in a zoo.

aggressive" (eg: A grabs feathers of B), "lower-cost aggressive" (eg: A displaces B from foraging spot), and "submissive" (eg: A falls to the ground in front of B and makes "crying call"). A ranking of individuals was made based on winning and losing interactions.

Overall, one-quarter of interactions were classed as "higher-cost aggressive", and another quarter as "lower-cost aggressive" with most of the remainder as "submissive". The expected general pattern was that individuals expressed aggression towards those below themselves in the dominance hierarchy and submission to those above themselves.

In terms of the specifics, "higher-cost aggressive" interactions were significantly more likely than chance towards individuals of equal or very similar rank, and significantly less likely towards individuals far below in the hierarchy. "Lower-cost aggressive interactions" were significantly less likely than chance towards equal ranks, and significantly more likely towards lower ranks. These findings supported the idea of "strategic aggression".

The researchers accepted the possibility of observational bias - ie: "higher-cost interactions are more conspicuous and therefore more detectable to a human observer using an all-occurrence sampling method" (Dehnen et al 2022 p9). This is a problem with behaviour or event sampling - ie: recording only certain behaviour/event every time it is seen - rather than point sampling which records what an individual is doing at a particular time.

The research depended on the accuracy of the ranking of individuals. A common method used in previous studies was employed. Basically, individuals are ranked on their perceived winning and losing of interactions, which is tallied up and converted into a position in the dominance hierarchy. Around one-third of the data were used in this process by Dehnen et al (2022). But McCowan et al (2022) included indirect information in their model of measuring the dominance hierarchy. For example, A and B directly interact, as do B and C, but A and C never interact. It is possible to infer the rank positions of A and C though, because, in this example, B submits to A, and C submits to B in direct interactions. So A outranks C.

1.5. CONSEQUENCES

The position in a social hierarchy is linked to physical condition (as opposed to nepotism - an individual's relatives). Being in good physical condition is important for high ranking individuals to be able to physically dominate others, and to cope with the stress of the demands of maintaining their position.

Baboons have been well studied here, as in a five-decade long field study in Kenya (Anderson et al 2022). Specifically, blood samples were available from ninety-seven adults. The cost of high-rank was greater for males (eg: elevated stress hormones), but the opposite for females (ie: low-ranked females were more stressed). Social status in male baboons is "driven almost entirely by fighting ability" (Anderson et al 2022 p7).

Even in the controlled environment of captivity, low-ranking individuals suffer shorter lifespans and health problems (Simons et al 2022).

In trying to establish the cause of the relationship between dominance/social status and health, Simons et al (2022) found that "rank-associated behavioural interactions" (eg: agonism; grooming) were better predictors than "dominance rank itself" (p1).

These researchers used data on 45 adult female rhesus macaques in nine social groups at the Yerkes National Primate Research Centre, USA. Observations were made of behaviour and interactions in early 2013 (Phase 1), and then the social groups were deliberately changed in 2014 (Phase 2). Simons et al (2022) explained that this change allowed the researchers "to observe the same females after most switched positions in the rank hierarchy between Phase 1 versus Phase 2: half became higher-ranking in Phase 2, while the other half became lower-ranking in Phase 2" (p3). This experiment was previously reported as Snyder-Mackler et al (2016).

During the observation period, trained researchers classified threats, attacks, and chases as agonistic interactions, and grooming (received and given - minutes per hour) as affiliative interactions. Together these behaviours led to a ranking in the dominance hierarchy.

1.6. COGNITIVE ABILITIES

Mental representation of the dominance order requires cognitive abilities (eg: to remember who is above and below yourself). But "in societies structured by different types of affiliated relationships, ranks may become dependent on the assistance/presence of individuals like kin, partners or friends. Such species are hypothesized to develop a third-party understanding, ie: they represent not only their own relationships but also the relationships between others" (Boucherie et al 2022 p2). This has been observed in non-human primates, and "various observational have indicated a strategical use of this knowledge, ie: planning alliances or preventing others from gaining rank" (Boucherie et al 2022 p2).

This seems to work best in stable groups. "In species expressing high degrees of fission–fusion dynamics, it may become difficult for individuals to keep track of their own and others' relationships" (Boucherie et al 2022 p2). Common ravens (Corvus corax) are "an interesting model species to study dominance under 'complex' dynamic social conditions: on one hand their foraging groups are characterised by moderate to high fission–fusion dynamics, on the other hand they are structured by age, breeding status and differentiated relationships" (Boucherie et al 2022 p2).

Boucherie et al (2022) analysed data collected on a wild raven population in the Austrian Alps between 2007 and 2019 (n = 183 individuals), and captive groups in Austria (n = 51). The basic rule-of-thumb from previous studies (eg: Braun and Bugnyar 2012) is that males dominant females, older birds dominate younger ones, and bonded birds dominate non-bonded birds. So, older males (who are larger) and more aggressive individuals should dominate overall.

This was supported by the data from Boucherie et al (2022) in both wild and captive groups. The ravens also showed evidence of "renowned cognitive skills" as the foraging groups, particularly in the wild, were "open and dynamic" (Boucherie et al 2022 p10). The ravens were able to maintain information about sex, age, and bonding categories, as well as mentally represent others' rank relationships (including inferring third-party relationships by observation only). All of this in groups that were unstable as members came and went over time (Boucherie et al 2022).

1.7. PHYSIOLOGY

There is interest in the physiological changes after dominance encounters, which can be different for the winner and the loser. For example, glucocorticoids (stress-related hormones) are elevated in both the winner and loser in interactions between male rainbow trout, but "this increase tends to be much longer lasting for losers" (Knoch et al 2022 p2).

Such studies require blood and tissue sampling, and have "some ethical and practical limitations, because it is invasive and requires capture and handling (or even sacrifice) of the animal. This creates a time lag from the event of interest to the sampling point and acts as an additional stressor, directly affecting the physiological measures of interest and potentially causing injury and infections. Time lags are also a problem for faecal sampling, a non-invasive method commonly used in field studies" (Knoch et al 2022 p2).

These problems led Knoch et al (2022) to use "stress-induced hyperthermia" (SIH) (or "psychogenic fever"). This is "a common response in endothermic animals to perceived threats in which sympathetically mediated vasoconstriction redirects peripheral blood flow towards the body core, raising core temperature" (Knoch et al 2022 p2). SIH has been found to correlate with levels of stress-related hormones, for instance (Knoch et al 2022).

Core body temperature has been measured in captive male great tits, for example (eg: Carere et al 2001), and it was found to be "elevated for 1 day after experiencing a social defeat, and defeated males also tended to avoid social interaction with conspecifics during this period. These studies induced social defeat using a resident-intruder paradigm, whereby an 'intruding' individual is introduced to the home cage of a 'resident' individual, with the latter almost always winning" (Knoch et al 2022 p2). This type of study measured temperature by inserting a probe down the throat (Knoch et al 2022).

SIH leads to a rapid drop in surface body temperature which can be detected through remote thermal imaging using infra-red cameras (or infra-red thermography; IRI). This was the method used by Knoch et al (2022) with 126 captive-reared juvenile pheasants (Phasianus colchicus) in the UK.

Baseline head temperatures were available for ninety-four pheasants. Eighty-five aggressive encounters were observed. Knoch et al (2022) summarised the findings thus: "head temperature dropped sharply in the few seconds prior to an attack, followed by an increase and then a more gradual decline back down towards baseline levels. Aggressors were on average slightly hotter than recipients, but the changes in temperature were similar for both roles" (p7). The fact that there was little difference between the aggressor and the recipient suggested that such interactions are equally stressful for both parties.

This study was "a first step" (Knoch et al 2022 p8) in using IRT to measure dominance interactions, but there was a lack of control over the interactions (as in the "resident-intruder paradigm"). Longer term and better baseline measures were needed (Knoch et al 2022).

1.8. NEURAL MECHANISMS

There is plenty of research on the neural mechanisms of aggression, but what about the neural mechanisms of establishing social rank? A crucial aspect of this is the awareness of own rank and that of others in the dominance hierarchy. Status signals are thus important.

There are two main types of signals (Dwortz et al 2022):

a) Chemical signalling - eg: pheromones; urinary proteins. The vomero-nasal organ (VNO) is the key brain area in detecting these.

For example, neurons in the VNO of mice (of both sexes) are more active upon sniffing urine from dominant than subordinate males (Dwortz et al 2022).

b) Visual signalling - eg: facial expressions. The amygdala is the key brain area here, and it is more active in macaques, for instance, in response to angry or threatening facial expressions of unfamiliar individuals. Amygdala lesions reduce this reaction (Dwortz et al 2022).

In primates, the dorso-lateral prefrontal cortex (DLPFC) also plays a role.

Learning of social rank is also relevant. "For example, in lizards, manipulating the dominance-signalling dark eyespot does not alter previously established dominant–subordinate relationships, but it does determine dominant–subordinate relationships between unfamiliar dyads. Furthermore, status signals do not explain how animals are able to detect subtle rank gradations that exist in highly linear dominance hierarchies where individuals behave differentially towards their two closest-ranking group members" (Dwortz et al 2022 p6). The neural mechanisms involved are the amygdala, hippocampus, and the dopaminergic system (Dwortz et al 2022).

Dwortz et al (2022) ended with the lament that "glaringly absent from our knowledge is how the female brain represents social rank and the neural underpinnings of how females negotiate social rank relationships. Much of the knowledge... stems from experiments conducted almost exclusively in male animals" (p9).

1.9. EUSOCIAL INSECTS

Eusocial insects show "reproductive division of labour" where certain "castes" are reproductive and the rest are not. But non-reproductives often still have the physiological potential for reproduction, and the dominance hierarchy represses it (Shimoji and Dobata 2022). "The resulting dominance hierarchies are remarkable for their size: the number of individuals in the hierarchy often reaches 70. The formation and maintenance of such large hierarchies would require unique selective forces that are not present in other animal societies" (Shimoji and Dobata 2022 p1).

Dominance behaviours can be observed in the three phases of a colony's life cycle (Shimoji and Dobata 2022):

i) Founding of the colony - In some species multiple potentially reproductive females are founders, but only one can actually reproduce in that colony. This is established by aggressive interactions between the foundresses, which could include the killing of the others.

ii) Maintenance - Both reproductive and non-reproductive individuals dominant lower-ranked non-reproductives to repress their reproductive potential. This may be done by behaviours or hydrocarbon profiles (ie: chemicals that can suppress the reproduction of others), for instance.

iii) Reformation - When the top-ranked reproductive female is lost, a new dominance hierarchy is formed.

Different attributes are involved in establishing dominance in eusocial insects. These include (Shimoji and Dobata 2022):

a) Age - Usually older individuals are dominant, but there are ants where younger individuals are higher ranked.

b) Physiology - eg: juvenile hormone levels; cuticular hydrocarbons (CHCs).

c) Past experiences of winning or losing in social interactions.

In understanding the evolution of subordination, one explanation is the "hawk-dove" scenario (Smith 1982). In any competitive interaction there are two possible strategies - attack (hawk) or submit/retreat (dove). The severe cost of both being hawks every time would favour a dove strategy for some individuals.

An alternative explanation is "social queuing" (Kokko and Johnstone 1999). "Subordinates are considered to 'make the best of a bad job' by waiting... to take over the top rank after the current dominant dies" (Shimoji and Dobata 2022 p6).

Inclusive fitness is another factor to mention. "With the notable exception of some colonies in Polistes paper wasps where foundresses are unrelated, dominance hierarchies of eusocial insects are typically composed of genetic relatives, and inclusive fitness benefit of subordinates explains why they accept their positions in the hierarchy. The resulting reproductive harmony enables their dominance hierarchies to achieve larger sizes than those in other animal societies" (Shimoji and Dobata 2022 p7).

1.10. VAMPIRE BATS

In some species, female social rank and hierarchy exist. Rank can influence fitness, and social bond formation, where social grooming is important. "For example, in groups with steep hierarchies, low-ranked individuals often direct grooming up the hierarchy, whereas in groups with shallow dominance hierarchies, grooming is often more symmetrical" (Crisp et al 2021 p2).

Crisp et al (2021) investigated this topic in female common vampire bats (Desmodus rotundus). Though social groups are fluid, individuals mix with non-kin regularly, and "tend to roost near preferred individuals that are also grooming and food-sharing partners. Regurgitated food sharing appears to be critical for vampire bats because they regularly fail to feed in the wild and have a poor capacity to store energy. Food donation rates are predicted by grooming, reciprocal donations and kinship, and new food-sharing bonds develop through escalations of reciprocal grooming. Vampire bats groom each other more than other bat species and social grooming is more frequent in females than males" (Crisp et al 2021 p2).

A captive colony of thirty-three bats (24 females) in Panama were observed over six months. Interactions at the feeders were video-recorded and categorised into five types of dominance behaviour:

i) Contact intrude - A feeding bat is physically removed by an intruder.

ii) No-contact intrude - As (i) but no physical contact.

iii) Contact defend - A feeding bat physically fends off an intruder.

iv) No-contact defend - As (iii) but no physical contact.

v) Waiting - A bat waits until the feeder is free to use.

Based on these categories, winners and losers were distinguished. In (i) and (ii) the winner is the intruder compared to (iii) and (iv) where it is the defender. The waiting bat is classed as a loser in (v). Winning and losing interactions were summed up as part of assigning of social rank to each individual.

In total, 1023 interactions at the feeder could be categorised. It was concluded that "female common vampire bats form a dominance hierarchy that is weakly linear and shallow, suggesting egalitarian access to resources among familiar bats" (Crisp et al 2021 p7). The researchers were not surprised that the dominance hierarchy appeared weak. "The fact that vampire bats regurgitate food to feed their close female associates suggests a lack of competition over food with preferred partners . That is, if an individual would give food to another, then there is no reason to use rank to monopolise that food. Socially bonded female vampire bats may also have higher fitness interdependence, meaning that each female might benefit from the survival and reproduction of other females in her group" (Crisp et al 2021 p9).

It was not possible to link social rank to physical differences between the bats. The researchers offered three non-mutually exclusive possibilities for this: "female social rank might not be driven by physical traits, individual ranks might not be sufficiently precise to detect effects, and winning rates might be more influenced by other factors such as winner–loser effects" (Crisp et al 2021 p8).

Another interesting finding was reported by Crisp et al (2021): "Contrary to patterns in some female primates, we found no evidence that females directed grooming or food sharing to higher-ranking females, or that rates of grooming, food sharing or their symmetry, were biased to closer ranked females" (p8).

This study has some limitations, not least that the colony was captive. Crisp et al (2021) explained: "In captivity, access to food is much easier than in the natural environment, where a bat must at some risk to itself first make an open wound by biting a much larger host animal that could suddenly attack or move away, and where every wound might also be taken over by other nearby conspecifics. By contrast, the bats in our study did not have to bite hosts, and the multiple blood-filled spouts could always be shared by individuals and were accessible during the entire night, so the benefits of competitive interactions were likely to be greatly reduced relative to the wild" (p9).

The observations of behaviour were sampled, and so the classifying of interactions and social rank could be imprecise. Also "displacement at the feeder" may not be a valid measure of dominance. Vocalisations were not measured either, and these may have mediated the dominance interactions.

1.11. THE FUTURE

Strauss and Shizuka (2022) outlined a number of key questions and issues that need further research based on three levels of analysis of dominance hierarchies:

1. Individual level

i) How and why do individuals change their position in the dominance hierarchy? For example, problems in measuring and explaining "social mobility".

"A crucial methodological decision when identifying social mobility is to determine the time period over which potential dynamics are assessed. The more frequently potential changes are assessed, the more potential changes can be found. For instance, assessing an individual's change monthly over a year can lead to the identification of 11 changes in position, whereas measuring mobility daily over the same period could potentially identify 364. Accordingly, sampling for dynamics more frequently leads to the identification of more changes. There are dangers to assessing potential changes both too frequently or too infrequently — if changes are assessed too rarely, real changes can be missed or misinterpreted (ie: false negatives), while assessing changes too frequently can lead to inference that is overly sensitive to uncertainty in an animal's relationships (ie: false positives)" (Strauss and Shizuka 2022 p4).

ii) How does dominance impact across life? It is difficult to study processes across the lifetime.

2. Dyadic level

i) When and why do dyads engage in contests? This "requires data that go beyond direct interactions - eg: initiation, avoidance, long-distance signals, behavioural state etc" (Strauss and Shizuka 2022 p2).

ii) How do dominance relationships form and dissolve? There is a need for "the development of interaction-to-relationship models of how repeated interactions with particular opponents are integrated to form relationships" (Strauss and Shizuka 2022 p5).

3. Group level

i) What are the causes and consequences of social instability? A need for accurate measures of "instability", while "rare but extreme instability can have high impact but be difficult to study" (Strauss and Shizuka 2022 p2).

1.12. REFERENCES

Anderson, J.A et al (2022) Distinct gene regulatory signatures of dominance rank and social bond strength in wild baboons Philosophical Transactions of the Royal Society B 377, 20200441

Boucherie, P.H et al (2022) Dominance in a socially dynamic setting: Hierarchical structure and conflict dynamics in ravens' foraging groups Philosophical Transactions of the Royal Society B 377, 20200446

Braun, A & Bugnyar, T (2012) Social bonds and rank acquisition in rven non-breeder aggregations Animal Behaviour 84, 1507-1515

Carere, C et al (2001) Effect of social defeat in a territorial bird (Parus major) selected for different coping styles Physiology and Behaviour 73, 427-433

Crisp, R.J et al (2021) Social dominance and co-operation in female vampire bats Royal Society Open Science 8, 210266

Dehnen, T et al (2022) Costs dictate strategic investment in dominance interactions Philosophical Transactions of the Royal Society B 377, 20200447

Drews, C (1993) The concept and definition of dominance in animal behaviour Behaviour 125, 283-313

Dwortz, M.F et al (2022) Neural systems that facilitate the representation of social rank Philosophical Transactions of the Royal Society B 377, 20200444

Hobson, E.A (2022) Quantifying the dynamics of nearly 100 years of dominance hierarchy research Philosophical Transactions of the Royal Society B 377, 20200433

Knoch, S et al (2022) Hot-headed peckers: Thermographic changes during aggression among juvenile pheasants (Phasianus colchicus) Philosophical Transactions of the Royal Society B 377, 20200442

Kokko, H & Johnstone, R.A (1999) Social queuing in animal societies: A dynamic model of reproductive skew Proceedings of the Royal Society of London B 266, 571-578

Lewis, R (2002) Beyond dominance: The importance of leverage Quarterly Review of Biology 77, 2, 149-164

Lewis, R (2022) Aggression, rank and power: Why hens (and other animals) do not always peck according to their strength Philosophical Transactions of the Royal Society B 377, 20200434

McCowan, B et al (2022) Measuring dominance certainty and assessing its impact on individual and societal health in a non-human primate model: A network approach Philosophical Transactions of the Royal Society B 377, 20200438

Schjelderup-Ebbe, T (1922) Observation on the social psychology of the domestic chicken Zeitschrift fur Psychologie
88, 225-252

Shimoji, H & Dobata, S (2022) The build-up of dominance hierarchies in eusocial insects Philosophical Transactions of the Royal Society B 377, 20200437

Simons, N.D et al (2022) Agonism and grooming behaviour explain social status effects on physiology and gene regulation in rhesus macaques Philosophical Transactions of the Royal Society B 377, 20200132

Smith, J.M (1982) Evolution and the Theory of Games Cambridge: Cambridge University Press

Snyder-Mackler, N et al (2016) Social status alters immune regulation and response to infection in macaques Science 354, 1041-1045

Strauss, E.D & Shizuka, D (2022) The dynamics of dominance:

Open questions, challenges and solutions Philosophical Transactions of the Royal Society B 377, 20200445

Strauss, E.D et al (2022a) The centennial of the pecking order: Current state and future prospects for the study of dominance hierarchies Philosophical Transactions of the Royal Society B 377, 20200432

Strauss, E.D et al (2022b) DomArchive: A century of published dominance data Philosophical Transactions of the Royal Society B 377, 20200436

Wallace, K.J et al (2022) Social ascent changes cognition, behaviour and physiology in a highly social cichlid fish Philosophical Transactions of the Royal Society B 377, 20200448

2. INFANT CORPSE CARRYING

"Comparative thanatology" is the study of non-human animals' responses to dead conspecifics and heterospecifics. A range of diverse behaviours have been reported from burial behaviour by some termites to feeding on corpses observed in Taiwanese macaques (Fernandez-Fueyo et al 2021).

Among primates, infant corpse carrying (ICC) has been reported, varying from very brief to mothers carrying the corpses past decomposition and mummification (Fernandez-Fueyo et al 2021). "ICC is prima facie a non-adaptive or maladaptive behaviour, as it is presumably energetically costly and hinders locomotion, foraging and predator evasive behaviour, but provides no obvious fitness benefit" (Fernandez-Fueyo et al 2021 p1).

Fernandez-Fueyo et al (2021) collected eighteen hypotheses to explain ICC from previous studies, and these can be placed in the following major categories:

i) Physiology of the mother causes care to continue after death - eg: hormonal hypothesis (maternal hormones related to infant care remain high even under the infant's death); maternal investment hypothesis or sex-biased maternal investment hypothesis (in some species maternal investment in their young is high, especially for one sex, and thus automatically continues after death).

ii) Mother-infant bond strength hypothesis - The strength of the attachment means that maternal behaviour continues after death.

iii) Aspects of dead infant still elicit care - eg: infantile cues hypothesis (the corpse still maintains the characteristics that elicit infant care); infant dependency hypothesis (the infant dies when its dependency is greatest and maternal behaviour continues after death).

iv) Grief management hypothesis - The physical contact of the corpse helps the mother in dealing with the stress of loss.

v) Mother unable to spot and/or unaware of death - eg: cause of death hypothesis or unawareness hypothesis (the cause of death is not clear to the mother such that care continues).

vi) Future benefits for continuing care - eg: learning to mother hypothesis (mothers gain valuable experience for future infants from continuing to carry the corpse) (table 2.1); death detection hypothesis (proximity to a corpse gives information to spot future infant death).

vii) Parity hypothesis - Previous experience in caring encourages continued caring after death.

viii) Caring for dead infant signals mother's quality - eg: mother rank hypothesis (only high ranking females can afford energetically costly demands of caring for a dead infant).

- Warren and Williamson (2004) reported two new observations of mountain gorillas in Rwanda. Firstly, ICC for 15 and 27 days in two cases (compared to the previously reported 2-4 days) by four adult females. Secondly, the never seen before, ICC by unrelated females.

- The latter behaviour fitted the "learning to mother" hypothesis as Warren and Williamson (2004) pointed out that "[P]ractice carrying and grooming need not involve live infants. For example, a sub-adult female mountain gorilla has been observed cradling a clump of moss and manoeuvring as if she was carrying an infant... It seems likely that the benefits of 'learning to mother' could be gained with a corpse, since the motor skills required to carry an infant while travelling and foraging could still be acquired" (p377).

Table 2.1 - Warren and Williamson (2004).

In terms of studies, Das et al (2019), for example, collated 43 cases of ICC from eighteen primate species, and found no relationship between infant sex or age at death, and length of ICC. Older mothers carried for longer. Also "infants that died of sickness or were stillborn being carried for longer than those that died of infanticide or those that died from electrocution or mother mishandling; arboreal primates carried for longer than terrestrial or semi-terrestrial primates; and semi-wild primates carried for shorter durations than captive, wild and urban primates" (Fernandez-Fueyo et al 2021 p4).

Fernandez-Fueyo et al (2021) compiled a database of ICC with 409 published cases from fifty primate species. Each case was scored on twelve variables, including mother's age, infant's age at death, and cause of death. The only variable that was significant was infant's age at death, with longer ICC for younger infant age at death. "This result may provide support for hypotheses that suggest that ICC is a by-product of a strong mother-infant bond" (Fernandez-Fueyo et al 2021 p1).

REFERENCES

Das, S et al (2019) Deceased-infant carrying in non-human anthropoids: Insights from systematic analysis and case studies of bonnet macaques (Macaca radiata) and lion-tailed macaques (Macaca silenus) Journal of Comparative Psychology 133, 156-170

Fernandez-Fueyo, E et al (2021) Why do some primate mothers carry their infant's corpse? A cross-species comparative study Proceedings of the Royal Society B 288, 20210590

Warren, Y & Williamson, E.A (2004) Transport of dead infant mountain gorillas by mothers and unrelated females Zoo Biology 23, 375-378

3. COMMUNICATION AND RECOGNITION

3.1. SQUID

Visual signals are an effective means of communication, but they require adequate levels of light to be seen. "The deep ocean is an all but totally dark environment and is thus not known to harbour animals that display complex visual signals beyond bioluminescent displays" (Burford and Robison 2020 p8524).

An exception is the complex visual signals of the Humboldt squid (Dosidicus gigas) (figure 3.1). Burford and Robison (2020) used electric remotely operated vehicles (ROVs) to video-record this species in deep waters in the Pacific Ocean off the US California coast between 2005 and 2012. Each of thirty individuals was observed for fourteen seconds at a time, and the chromatic displays were categorised. This species of squid is not scared of ROVs unlike others (Burford and Robison 2020).

(Source: NOAA/MBARI 2006; public domain; https://oceanexplorer.noaa.gov/explorations/06davidson/logs/summary/media/squid_600.html)

Figure 3.1 - Humboldt squid.

The variable chromatic displays of "flashing" (a rapid change between pale and dark) and "flickering" ("dynamic mosaic of scattered pigmentation") were observed when foraging in groups. These displays were sub-divided into twenty-eight components (along with eight postural and five locomotive components).

The researchers also found that the squids illuminated themselves to make the visual signals visible in the dark ocean ("bioluminescent backlighting"). "Numerous small sub-cutaneous... photophores (bioluminescent organs) embedded throughout the muscle tissue make the entire body glow, thereby backlighting the pigmentation patterns" (Burford and Robison 2020 p8524).

Burford and Robison (2020) concluded that "the chromatic behaviours displayed by a deep-living social squid could share design features with advanced forms of animal communication, as specific components seem to be tied to specific contexts (semanticity) and may be combinable in distinct ways (discreteness). Both features are indicative of signal complexity — the latter suggesting that multiple components may interact with one another to alter the message they convey, but not precluding the possibility that some components could elicit behavioural responses on their own" (p8527). The researchers could not record the behaviour of recipients to confirm this point.

In terms of the evolution of these signals, Burford and Robison (2020) described a combination of content-based and efficacy-based selection pressures (Guilford and Dawkins 1991). The former refers to pressures that maximise information content. "The ability for individuals to rapidly signal foraging intent and competitive quality... could help avoid antagonistic interactions in dense foraging aggregations" (Burford and Robison 2020 p8527). Efficacy-based pressures refer to those that facilitate information transfer (eg: environmental variability).

3.2. HYENA AND VISUAL COMMUNICATION

Communication is based on signals, which convey information about characteristics of the sender (eg: body size; sex) and the content (eg: motivation of sender). Signal optimisation theory proposes that specific features of signals evolve to maximise signal success (ie: to change the receiver's behaviour) (Nolfo et al 2021).

This is especially important when two behaviours are very similar, like fighting/aggression and play fighting/social play in mammals. "During social play, the motivational and intentional state of an individual can be expressed to a groupmate through the relaxed open mouth (ROM) display, which is considered a ritualised signal... that simulates the intention to bite during playful interactions in mammals" (Nolfo et al 2021 p2). Other signals are also used in play fighting, including head bobbing (HB).

Concentrating on wild spotted hyenas (Crocuta crocuta), Nolfo et al (2021) investigated ROM and HB. The researchers made five predictions based on signal optimisation theory:

i) The receiver must be attentive to the sender - So, ROM and HB will be performed when there is direct visual contact (Prediction 1).

ii) The context of the signals - ROM is specific to play fighting and will be seen only in this context, whereas HB occurs more generally in positive social interactions (Prediction 2).

iii) Signals have underlying messages ("meta-communication" according to Bateson 1951) - This means that ROM and HB should precede physical contact to signal play rather than conflict (Prediction 3), continue throughout (Precision 4), and work together (Prediction 5).

The data were 36 hours of video recordings of sixty-four hyenas at a private game reserve in South Africa collected in 2019. The focus was upon 24 individuals where there was at least thirty minutes of video recordings each.

All the 46 ROM and 63 HB events observed were performed when the sender had direct visual contact with the receiver. Prediction 1 was thus supported. Horowitz (2009) referred to the "attention to attention condition" as a building block of intentional communication (ie: being aware that the receiver is looking in your direction before signalling) (Nolfo et al 2021).

After ROM events, play fighting occurred significantly more often than other positive social interactions, while there was no difference after HB events, which supported Prediction 2. Head gestures have been observed to be used in more than one context among monkeys, for example (Nolfo et al 2021).

Predictions 3 and 4 were partially supported, but Prediction 5 was not supported. ROm events occurred before and during play fighting, whereas the pattern for HB events was less clear, and HB and ROm events were not correlated. Nolfo et al (2021) stated that their findings were "the first empirical evidence that a facial expression (ROM) can be used as a meta-communicative signal in wild spotted hyenas. The use of signals in clarifying the intentions of animals during play... seems to acquire even more importance in species whose play modality is rough and competitive" (Nolfo et al 2021 p6).

In summary, visual signals were found to be important in the management of play fighting.

3.3. SEAHORSES AND MATE RECOGNITION

Lin et al (2021) explained: "Seahorses (Hippocampus spp) are unique species known for male pregnancy... The female deposits her eggs into the male's brood pouch, where they are fertilised, and then all care is provided by the male. Males protect, aerate, nourish and osmoregulate developing embryos throughout pregnancy before releasing them as independent young... In addition to their unique reproductive mode, seahorses are also known for their monogamous mating system" (p1).

Paired male and female individuals remain separate after breeding except for a brief ritualised interaction each day (called "daily greetings" or "morning greetings"). "They brighten their body colours, swim parallel to each other (aligned head to head and tail to tail), and circle in the same direction from time to time" (Lin et al 2021 p1).

Recognition of the mate is important in monogamy. What cues are used by seahorses? Vincent (1995), which Lin et al (2021) suggested was the only study on the topic before their own, found that females preferred males who they had greeted regularly, suggesting that behaviour cues were important.

Lin et al's (2021) experiments involved captive-bred lined seahorses (Hippocampus erectus) (figure 3.2) at a research institute in China. The researchers compared behavioural, visual, and olfactory cues in mate recognition by varying them.

(Source: Marco Aimbauer; in public domain)

Figure 3.2 - Lined seahorse.

In Experiment 1, behavioural cues (ie: greetings) were blocked, but not the other two cues. Females remained faithful to their mate when offered a choice of males despite this block, which contradicts the Vincent (1995) study.

In Experiment 2, the olfactory cues were blocked by putting individuals in transparent plastic bags, and this retained the visual cues. Females showed no preference for their mate over another male, which suggested the role of olfactory cues in mate recognition.

Details of the different experimental conditions are given in table 3.1.

- The experiments used paired seahorses and the focus was upon the female choice for another breeding (which in the wild would be the same male).

Experiment 1:

- A (control condition) - Female offered choice of mate and another male; 9 of 10 chose mate.

- B (blocked greeting condition 1) - Female in wire mesh cage which stopped daily greeting, but could see and smell mate.

When given choice of mate and another male, 7 of 10 chose mate.

- C (blocked greeting condition 2) - Mate and another male in wire mesh cage to stop greeting. 8 of 10 females chose mate.

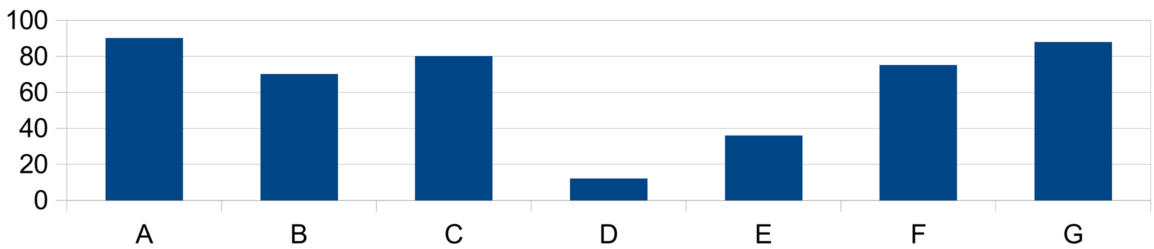
Experiment 2:

- D (blocked olfactory cues 1) - Female in a transparent plastic bag filled with water could see mate and another male. Only 1 of 8 females chose mate.

- E (blocked olfactory cues 2) - Mate and another male in transparent plastic bag. 3 of 8 females chose mate.

- F (blocked visual cues 1) - Mate hidden from female in pipe in tank while another male was visible to her. Olfactory cues not blocked in the water. 6 of 8 females chose mate.

- G (blocked visual cues 2) - Mate and other male hidden in pipe. 7 of 8 females chose mate.



Percentage of females choosing mate in each condition.

Table 3.1 - Different experiments and conditions in Lin et al (2021) study.

3.4. PENGUINS AND CROSS-MODAL INDIVIDUAL RECOGNITION

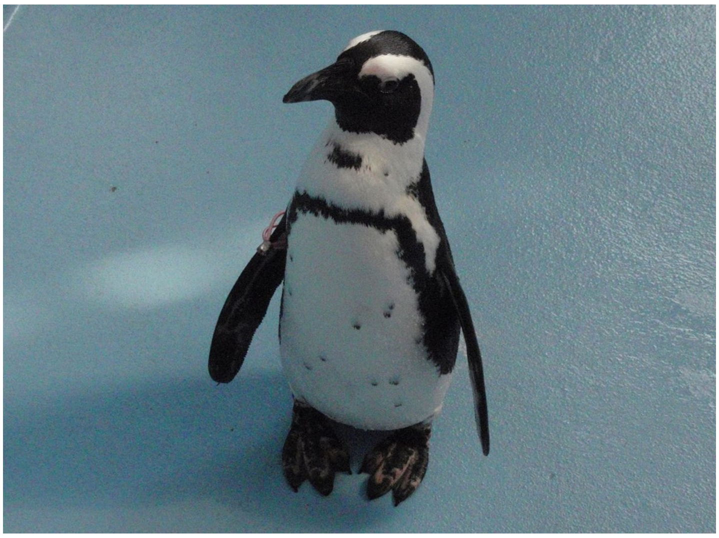
As well as recognising a familiar voice, humans can visualise the speaker if they are not physically present. This is known as "cross-modal individual recognition" (Baciadonna et al 2021).

Do non-human species have this ability? The problem is how to test for it, first and foremost, but the "expectation violation paradigm" is commonly used. The focal animal is presented with a familiar conspecifics visually, but another's vocalisation is played via a loudspeaker at the same time. The hearer should behave differently to this incongruent sensory information than when congruent information is presented (ie: the visual and auditory matched). In such a study with horses (Proops et al 2008), "the focal horse responded more quickly and looked significantly longer in the direction of the call than when the call matched the familiar horse they had just seen. This result suggests that the incongruent combination violated the focal horse's expectations and indicates that they recognised the other horse across sensory modalities as a unique individual" (Baciadonna et al 2021 p2).

Auditory-visual cross-modal individual recognition of conspecifics has been found in a few mammals, including African lions, goats, and rhesus monkeys, and auditory-olfactory cross-modal recognition in lemurs. Cats, dogs, and rhesus monkeys show auditory-visual cross-modal recognition of humans (Baciadonna et al 2021).

Crows have been studied and shown the ability to recognise group members (but not non-group members) among birds and non-mammals (Kondo et al 2012).

Baciadonna et al (2021) investigated this ability with the African penguin (Spheniscus demersus) (figure 3.3). Individuals have a distinctive and unique pattern of black spots on their chests (visual cues), and are colonial, territorial, monogamous seabirds (familiarity with other individuals).



(Photograph by Cassiopeia Sweet; in public domain)

Figure 3.3 - African penguin.

Ten penguins housed at a zoo in Italy were studied. Individual calls were first recorded. Then over a period of six months, each individual was tested in six different conditions:

i) Partner and own call (congruent P).

ii) Partner and another's call (incongruent P).

iii) Familiar same-sex non-partner colony-mate and own call (same-sex congruent NP).

iv) Familiar opposite-sex non-partner colony-mate and own call (opposite-sex congruent NP).

v) Familiar same-sex non-partner colony-mate and another's call (same-sex incongruent NP).

vi) Familiar opposite-sex non-partner colony-mate and another's call (opposite-sex incongruent NP).

The expectancy violation procedure was as follows: Two penguins were left alone in a small arena for one minute, then a keeper removed one of them through a small opening, and a call was played as soon as the penguin was out of sight. The behaviour of the focal penguin was video-recorded and subsequently analysed (eg: duration of looking; movement towards the loudspeaker).

Baciadonna et al (2021) explained their expectations for the study: "If penguins possess multi-modal representations of other individual penguins, then after seeing a familiar conspecific, the presentation of a mismatched auditory cue should violate their expectations and result in differences in their reactions to the incongruent calls compared to the congruent calls. We further predicted that because penguins should have greater familiarity with their own partners compared to other colony members, the observed differences in their reactions should be larger for the partnered situation, ie: when the focal penguin and stimulus penguin are partners, compared to the non-partnered situation" (p4).

The penguins responded by looking towards the loudspeaker significantly faster in the incongruent NP conditions than the congruent NP conditions, but there was no difference in the P conditions. "However, when the auditory calls were congruent with the stimulus penguin, focal penguins looked nearly five times faster in response to their partner's call... compared to a non-partner's call... suggesting that the partner-related cues may in general prompt stronger behavioural reactions" (Baciadonna et al 2021 p4). Duration of looking was not different between the conditions.

Cross-modal recognition makes sense in this species as "African penguins are territorial, but partners nest quite close to their colony-mates. Therefore, the ability to identify one's friendly neighbours both visually and vocally may have evolved to help reduce unnecessary conflicts. In addition, during the breeding season, one of each partner pair always stays at the nest with the eggs while the other hunts with the colony. Cross-modal recognition may have proved valuable in the turbulent environment among the waves and rocks, where visual identifiers, eg: their unique pattern of black spots, may not be a reliable salient cue to recognise others. Therefore, to better co-ordinate and maintain contacts during hunting sessions, other cues were necessary, eg: vocal calls" (Baciadonna et al 2021 p5).

However, it was surprising to the researchers that the penguins did not respond differently in the P conditions, and Baciadonna et al (2021) speculated that other senses are involved (eg: auditory-olfactory cross-modal recognition).

The researchers offered another explanation as well: "African penguins spend most of their free time very close to their partner compared to their colony-mates, and more importantly their partnerships are monogamous and last their entire lifetime. It may be that in an expectancy violation paradigm where the stimulus penguin is a partner and is removed suddenly, the focal penguin is consequently put in a state that causes them to respond to any call very quickly (eg: increased attention, vigilance, anxiety etc). In normal states, penguins' responses to their partner's calls are stronger than to calls of non-partners. In our experiments, within the congruent condition, the latency to respond to a partner's call (mean 4.23 s) was nearly five times faster than to a familiar non-partner's call (20.90 s), highlighting the much greater saliency of a partner's call. Our proposed 'partner separation effect' may be worth investigating on its own" (Baciadonna et al 2021 p5).

A "preference looking paradigm" may have been a better method to use. This is where the focal individual is presented with two stimuli simultaneously, and the direction of looking is measured. "Here, the focal animal can keep their partner, and a non-partner, constantly in view. Their behavioural responses can then be measured to a vocal call that belongs to one of the other two penguins. However, a design like this would be quite difficult to implement in wild animals because it requires capturing and holding three subjects within a small and restricted area" (Baciadonna et al 2021 p5).

3.5. MOUSE

Mice, for example, use smell in many situations including feeding, mating, fighting, and predator escape. The internal state of the animal (eg: hunger) influences smelling (eg: sniffing rate; sensitivity to novel odours) (Horio and Liberles 2021).

Horio and Liberles (2021) placed a mouse in an arena with an odour port at each end from which different odours were released, and a preference index was calculated (based on the time spent at one end of the arena compared to the other). A preference index of zero means no difference in time spent at each end. This is a two-choice experiment.

For example, one odour was food (familiar home-cage chow dissolved in water), and the other pheromones (urine of an opposite-sex mouse). Recently fed mice showed no preference between the two odours (preference index = 0), while hungry mice displayed a strong preference for the food odour (preference index = 15-20).

Investigating the physiology, Horio and Liberles (2021) found that mice lacking neuropeptide Y (NPY) in the hypothalamus-thalamus circuit of the brain had a preference index of zero when hungry between food and pheromone odours. While injection of NPY into fed mice produced a preference for food odours.

This research showed that key internal states influence the sensitivity of the olfactory system in mice.

3.6. MOLE-RATS AND MAGNETIC SENSE

Magnetoreception is "the ability to perceive magnetic fields" (Caspar et al 2020 p1). It is better studied in birds than mammals [2]. Magnetite crystals (Fe_3O_4) are believed to be important in the body (eg: as studied in Ansell's mole-rat; Fukomys anselli) (figure 3.4) (Caspar et al 2020). These subterranean rodents from the woodlands of central Zambia have a preference to make nests in a south-eastern sector of a circular arena (Caspar et al 2020). Studies have established that the mole-rat's "magnetic compass" "works in total darkness and responds to changes in field polarity but not in inclination; it is affected by strong magnetic pulses but

[2] For example, cryptochrome 4 (CRY4) is a protein in the retina of birds that is sensitive to magnetic fields. Xu et al (2021) showed the the CRY4 was more magnetically sensitive in the night-migratory European robin than in two non-migratory bird species - the chicken and the pigeon. This research studied the protein in vitro (ie: in the petri-dish rather than in the animal).

is insensitive to radio-frequency magnetic fields" (Caspar et al 2020 p2).

(Source: Anfimo; in public domain)

Figure 3.4 - Ansell's mole-rat.

Where in the body is the "magnetic compass"? The eye has been studied in birds, and this organ was the focus of Caspar et al's (2020) study with Ansell's mole-rats.

The eyes of six adults were surgically removed (enucleation). Before the operation, in a circular arena, the mole-rats showed a preference to make nests in the south-eastern sector (as previously established), but after the operation the preference was random.

In another experiment with ten enucleated, the magnetic fields were experimentally manipulated. Prior to the operation, the nest preference was always in the magnetic south-eastern sector, and random after the operation. The conclusion of these studies was that "mole-rats perceive magnetic fields with their minute eyes, probably relying on magnetite-based receptors in the cornea" (Caspar et al 2020 p1).

Considering the ethics of the experiments, the researchers argued that "enucleation has no perceivable influence on mole-rats' behaviours apart from affecting magnetoreception..." (Caspar et al 2020 p5).

3.7. REFERENCES

Baciadonna, L et al (2021) Cross-modal individual recognition in the African penguin and the effect of partnership Proceedings of the Royal Society B 288, 20211463

Bateson, G (1951) Information and codification; and conventions of communication. In Ruesch, J & Bateson, G (eds) Communication: The Social Matrix of Psychiatry New York: W.W Norton & Co

Burford, B.P & Robison, B.H (2020) Bioluminescent backlighting illuminates the complex visual signals of a social squid in the deep sea Proceedings of the National Academy of Sciences, USA 117, 15, 8524-8531

Caspar, K.R et al (2020) Eyes are essential for magnetoreception in a mammal Journal of the Royal Society Interface 17, 20200513

Guilford, T & Dawkins, M.S (1991) Receiver psychology and the evolution of animal signals Animal Behaviour 42, 1-14

Horio, N & Liberles, S.D (2021) Hunger enhances food-odour attraction through a neuropeptide Y spotlight Nature 592, 262-266

Horowitz, A (2009) Attention to attention in domestic dog Canis familiaris dyadic play Animal Cognition 12, 107-118

Kondo, N et al (2012) Crows cross-modally recognise group members but not non-group members Proceedings of the Royal Society B 279, 1937-1942

Lin, T et al (2021) Female lined seahorses (Hippocampus erectus) recognise their mates based on olfactory cues Behavioural Processes 189, 104419

Nolfo, A.P et al (2021) Visual communication in social play of a hierarchical carnivore species: The case of wild spotted hyenas Current Zoology (https://academic.oup.com/cz/advance-article/doi/10.1093/cz/zoab076/6371184)

Proops, L et al (2008) Cross-modal individual recognition in domestic horses (Equus caballus) PNAS 106, 947-951

Vincent, A.C.J (1995) A role for daily greetings in maintaining seahorse pair bonds Animal Behaviour 49, 258-260

Xu, J et al (2021) Magnetic sensitivity of cryptochrome 4 from a migratory songbird Nature 594, 535-539

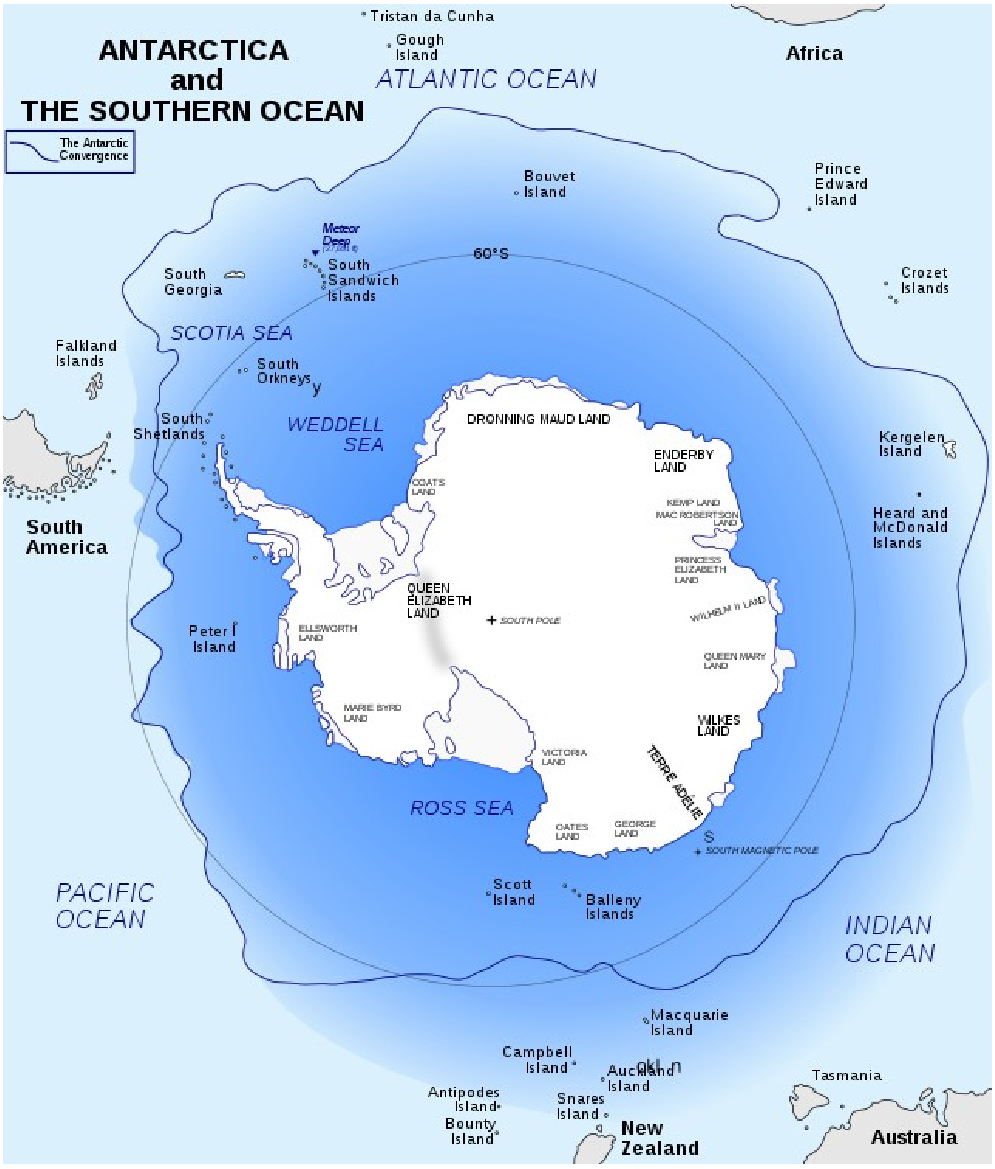
4. RESPONDING TO ENVIRONMENTAL CHANGE

4.1. OCEAN PROTECTION

The Southern Ocean (ie: the ocean region encircling Antarctica)(figure 4.1) has many unique animals (eg: Antarctic krill), but there is great concern about the impact of climate change upon it (Sequeira 2020) [3].

Tracking top predators can help to understand the state of an ecosystem. Hindell et al (2020) reported data from over 4000 individuals of seventeen species of marine predators (seabirds and mammals) in the Southern Ocean (between 1991 and 2016). Modelling from these data allowed the researchers to show the pressure from humans (ie: fishing) and climate change on the area, and confirm that the species at the base of the food web (eg: krill) were of most importance. Hindell et al (2020) recommended increasing the size of the protected areas (areas of ecological significance; AESs) in the Southern Ocean.

[3] The United Nations Sustainable Development Goal 14 (UNSDG14) is to "conserve and sustainably use the oceans, seas and marine resources for sustainable development" (quoted in Duarte et al 2020).



(Source: Hogweard)

Figure 4.1 - The Southern Ocean.

4.1.1. Twilight Zone

The "twilight zone" (TZ) is the area of the ocean where sunlight is beginning to fail to reach (200 - 1000 metres down) (Martin et al 2020).

This area is "almost pristine" compared to the impact of humans on coastal waters (Martin et al 2020).

Phytoplankton growing above the TZ in the sunlit area fuel the food chain in the TZ. Knowledge, however, is limited, partly because of the pressure of up to 100 atmospheres in the TZ (Martin et al 2020).

Martin et al (2020) outlined three areas of priority to investigate:

i) How many organisms live in the TZ? Estimates for the volume of fishes vary between one and twenty billion tonnes (compared to the total human population of 0.5 billion tonnes) (Martin et al 2020).

ii) What ecological processes occur in the TZ? (eg: "marine snow" - "sinking aggregates of organic material"; Martin et al 2020 p27).

iii) The movement in and out of the TZ.

4.1.2. OECMs

The "30 x 30 movement" is campaigning to conserve 30% of the planet by 2030 (Gurney et al 2021). Crucial to the success of such a campaign will be "other effective area-based conservation measures" (OECMs), which were devised in 2010 as different to "protected areas" (Gurney et al 2021).

"Protected areas" cover around 15% of land and freshwater, and 8% of the marine environment, while for OECMs it is less than 1% and 0.1% respectively (Gurney et al 2021). OECMs are more flexible and allow for hunting, fishing, and other cultural practices of local communities and Indigenous groups, whereas "protected areas" can end up excluding local communities (Gurney et al 2021).

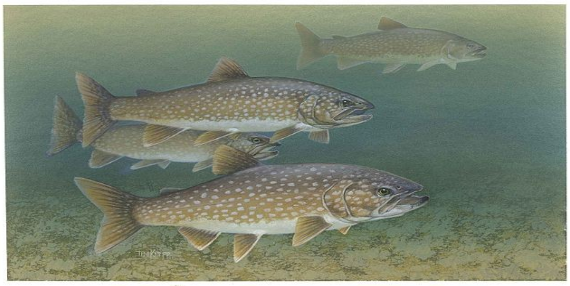
4.1.3. Icefish

A breeding colony of Jonah's icefish (Neopagetopsis ionah) has recently been discovered by underwater camera surveys on the floor of the southern Weddell Sea, Antarctica (Purser et al 2022). A vast number of nests (tens of thousands) were observed with one adult guarding over 1500 eggs in each nest. This provides a key food source for the ecosystem, both in terms of live and dead fishes.

"This discovery provides support for the establishment of a regional marine protected area in the Southern Ocean under the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) umbrella" (Purser et al 2022 p842).

4.2. FISH BRAIN

Some fishes experience seasonal fluctuations in temperature, light availability, and habitats. Versteeg et al (2021) investigated this in lake trout (Salvelinus namaycush) (figure 4.2), and, in particular, changes in brain size.



(Source: Knepp Timothy, US Fish and Wildlife Service; in public domain)

Figure 4.2 - Lake trout fishes.

"Brain and brain region size is correlated with performance in cognitively demanding tasks... and with variation in neuron numbers... As such, brain size variation is generally conceived as relating to variation in cognitive demands (ie: sensory, motor, and integrative functions)" (Versteeg et al 2021 p2). So, it was hypothesised that seasonal changes in cognitive demands would drive changes in brain size (both overall and specific areas). The brains of trout from two lakes in Canada between 2017 and 2019 (covering six seasons) were measured post-mortem.

Overall brain size was larger in autumn and winter compared to spring and summer, while the telencephalon area of the brain showed this pattern strongest. This area is related to spatial processing. The fishes have to navigate through more cognitively demanding environments in the autumn onto spawning shoals, while "also co-ordinating complex social behaviours during mating" (Versteeg et al 2021 p6). During the winter navigation takes place under reduced light conditions due to shorter daylight hours, and snow and ice cover of the lakes. In spring and summer the trout navigate deeper water which is less cognitively demanding. The findings supported the hypothesis that brain size changes with cognitive demand.

Previously, McCallum et al (2014) had reported that the telencephalon increased in size in the mating season in round goby (Neogobius melanostomus).

4.3. SEALS

"Ice is a key environmental driver for many polar organisms, with glaciers, snow, and sea ice often determining the size and connectivity of populations through diverse mechanisms. Ice can influence populations directly by creating or restricting access to potential habitat areas" (Cleary et al 2021 p14003). Ice is changing in the Antarctic, and information about historical changes can help plan for the future. Cleary et al (2021) looked at the Last Glacial Maximum (LGM) (approximately 25-15 000 years ago), and Antarctic fur seals (Arctocephalus gazella) using genomic data. These seals are "concomitantly reliant on both ice-associated prey and ice-free coastal breeding areas" (Cleary et al 2021 p14003).

Genomic data were ascertained from fifty-two seals in four present-day breeding colonies around the Antarctic (South Shetlands, South Georgia, Bouvetøya, and Iles Kerguelen). It was predicted that with the expansion of the ice sheet in the LGM, the population size of seals declined.

From the genomic data it was possible to show that the population split into sub-populations around the time of the LGM. Cleary et al (2021) explained: "As the ice extent increased, much of this area became uninhabitable, and the global population was reduced to two small refugial sub-populations, one in the west and one in the east. Refugial areas would have needed ice-free breeding habitat and productive foraging grounds, with potential locations north of present breeding areas or in areas with geothermal activity. After the ice declined, the western refugial population founded colonies at the South Shetlands, South Georgia, and Bouvetøya, while the eastern refugial population colonised Iles Kerguelen" (p14008).

In the future it is expected that the ice sheet will decline, but history has shown that these seals can establish new breeding colonies, despite their strong site fidelity. Cleary et al (2021) ended that "it may therefore be worthwhile giving conservation consideration to potential future breeding locations, such as areas further south along the Antarctic Peninsula, in addition to present colony areas" (p14009).

4.4. EQUINES

4.4.1. Ecosystem Engineers

Biopedturbation is a way that animals impact their environment. This is "the disturbance of soils by animals", and it "contributes to the ecosystems' diversity and heterogeneity" (Wagner et al 2021 p13036). Wagner et al (2021) outlined the different effects of the disturbance: "create vegetation-free areas, shape soil topography, alter soil density and structure, change infiltration properties and soil moisture, influence the nutrient situation, and contribute to carbon cycling and nutrient turnover" (p13037). The most common forms are burrows, mounds, and foraging digs (Wagner et al 2021).

Large mammals can cause ground disturbances by depressions in the ground from self-grooming resting (eg: American bison wallows; dust-bathing by donkeys).

Soil disturbance is even more important in arid environments. Depressions from resting mammals "collect run-off after rain and have better infiltration properties, increased soil moisture, and a higher nutrient content due to the accumulation of dung and urine" (Wagner et al 2021 p13037). Thus, soil-disturbing animals have been called "ecosystem engineers" (Wagner et al 2021). Coggan et al (2018) listed 121 such species.

Wagner et al (2021) added the Hartmann's mountain zebra (Equus zebra hartmannae) (figure 4.3), which lives in the semi-desert of south-west Africa (the Pre-Namib). These animals show a "unique dust-bathing behaviour" in "rolling pits". The researchers collected data between 2014 and 2018 in Namibia. All rolling pits in a certain area were mapped in 2014 (n = 656), and the vegetation was measured subsequently.

The vegetation composition was different and denser in the pits than in surrounding comparison areas. More arthropods were also attracted to the pit areas, "which in turn increased the activity density of omnivorous and predatory arthropods" (Wagner et al 2021 p13036).

The zebras were "ecosystem engineers" that contributed to the diversity of the landscape.

(Source: Ltshears - Trisha M Shears; public domain)

Figure 4.3 - Resting captive Hartmann's mountain zebra.

4.4.2. Digging Wells

In dry ecosystems, animals face challenges over water availability. But some large terrestrial herbivores may increase water availability by exposing sub-surface water (ie: "dig wells").

Lundgren et al (2021) reported observations of wild donkeys (Equus africanus asinus) and horses (Equus ferus caballus) in the Sonoran and Mojave Deserts in the USA. Four groundwater-fed stream sites were observed over three summers, and it was found that equid wells provided a large amount of the surface water. Other animals were also video recorded drinking at the sites.

Lundgren et al (2021) explained: "Stream intermittency is projected to increase as currently perennial streams lose yearlong flows and as drylands expand as result of groundwater mining, agriculture, and climate change. These reductions in water availability, coupled with rising temperatures, are projected to have strong effects on biodiversity and ecosystem function. Our results suggest that equids and other well-digging megafauna have the potential to mitigate these changes, whether native or introduced" (pp493-494).

4.5. ANTS

Longitudinal data are more important than ever to understand the impact of climate change on different animals. But there is a dearth of such studies, mostly because of the cost. The alternative is to combine multiple datasets, but there are issues with this method, including sampling differences, species bias, and identification errors (Sheard et al 2021).

Notwithstanding these problems, Sheard et al (2021) combined seven datasets to understand long-term changes in occupancy of areas by 29 Danish ant species from 1900 to 2019. The datasets included museum and personal collections, and researcher and citizen surveys, and covered four years to one hundred years.

Overall, five species increased in occupancy, four declined, six fluctuated, and fourteen were stable over the study period. Occupancy refers to the presence of the ants in areas where expected or previously found.

Sheard et al (2021) commented: "We find declining species are associated with dry, undisturbed habitats and open forests and have protein-rich diets, whereas increasing species are wet- and disturbance-tolerant and tend to be omnivores. These trends appear to be directly linked to changes in habitat and climate" (p4). So, the impact of climate change is "more complex than implied by the simple insect decline narrative" (Sheard et al 2021 p1).

4.5.1. Temporary Caching

Army ants forage in long columns of workers roaming forest floors and raiding the broods of colonies of other social insects. One species of such ants, the hook-jawed army ant (Eciton hamatum) accumulate the collected brood prey in temporary caches along their columns (de Lima et al 2022).

What is the purpose of these caches? Many researchers saw them as unimportant, as a byproduct of "traffic management" as ants move back and forth. But de

Lima et al (2022) argued that the "caches increased the amount of prey that relatively low numbers of raiders were able to retrieve" (p1). It is a strategy of "maximum prey retrieval": "From a colony-level perspective, short sequential trips between caches and foraging fronts would maximise prey yields at limited number of raiders" (de Lima et al 2022 p2). The advantage of temporary caching compared to returning home with each item of prey declined with more raiders.

The researchers observed ants in Brazil, video-recorded the behaviour, and then designed computer simulations.

4.6. RED-BACKED FAIRYWRENS

Wildfires are expected to increase with climate change in frequency and severity. What will be the impact on wildlife? Boersma et al (2021) studied the red-backed fairywren (Malurus melanocephalus) (figure 4.4) for answers.

Animals face a trade-off between reproduction and survival, and for males, this is manifest in testosterone levels. Testosterone is "essential for spermatogenesis and expression of mating behaviour, but elevation of testosterone can come with a host of detrimental effects to survival via endogenous costs including immunosuppression and external costs like increased predation and injury... The expression of secondary sexual characters like plumage ornamentation are stimulated by testosterone in males of many bird species..., and these ornaments can impose costs in the form of increased predation" (Boersma et al 2021 p2).

Boersma et al (2021) investigated testosterone, ornamentation, and naturally occurring wildfires in tropical north-east Queensland in 2012. Data were available on the fairywrens at a site called "Donkey Farm" prior to the wildfire as well as afterwards. Males have an ornamental black-and-red plumage, and this was scored (0-100) for individual birds. Testosterone levels were established from blood samples of netted birds.

Overall, males were significantly less ornamented (ie: lower score for plumage) in the fire year compared to a drought/dry year and the typical wet/monsoon year. There was lower testosterone in the fire year compared to the other years.

So, the wildfire suppressed plasma testosterone levels and consequently the development of ornamental plumage in young males. "These results are consistent with this species acting to maximise survival through changes in testosterone when a natural disturbance destroys breeding territories" (Boersma et al 2021 p8).

Other studies of red-backed fairywrens after wildfires have reported decreased reproductive output (ie: less offspring), and "reduced dawn singing following wildfire, indicative of a reduction in behaviour associated with breeding" (Boersma et al 2021 p7).

(Source: Nevil Lazarus)

Figure 4.4 - Red-backed fairywren.

4.7. HONEYBEE

Bees face the challenge of habitat loss with "extensive conversion of flower-rich habitat to land that is often nutritionally barren from the bee's perspective" (Ash et al 2022 p79), as well as pesticides, and emerging parasites and disease.

Contrary to common sense, bees may thrive in flora-rich patches within cities and towns as compared to in agricultural land. Ash et al (2022) investigated how the bees viewed these habitats by analysing the waggle dance of the western honeybee (Apis mellifera) in south-east

England.

The waggle dance of a bee returning to the colony after foraging communicates the location of resources. "Waggle dances encode both the distance to the resource (in the duration of the 'waggle' run) and its direction, relative to the sun's azimuth (in the angle of the dance relative to gravity...). Foragers do not dance to report every resource that they find, but only those that pass a quality threshold..., performing more circuits for resources that offer high energetic efficiency (ie: energy invested in travel - energy gained through food intake...). In other words, the closest highly rewarding sites elicit the most dances and thus the most recruits, and support for those sites builds within the hive through a positive feedback loop" (Ash et al 2022 p80). The work of von Frisch (1967) set the foundation for decoding the waggle dance.

The researchers studied twenty hives either in urban or agricultural sites in or around London over twenty-four weeks in 2017. Nearly 3000 dances were analysed from video-recordings.

It was estimated that the bees flew further on average to forage in agricultural landscapes than urban ones (median: 743 vs 492 metres). "The overall increased foraging distances covered by bees in agricultural land were not recompensed by increased nectar sugar content, which did not differ significantly between the two land-use types. In other words, agricultural bees did not fly further to exploit distant but richer nectar resources than those available to their urban counterparts, but rather, typically came back with similar quality forage, at least in terms of nectar concentration" (Ash et al 2022 p84). This suggested that bees were in a better position in the urban areas, and this was due to the modern agricultural landscape which is nutritionally barren for them.

These researchers were interpreting the bee's dance as the measure of direction and distance, which could have been over- or under-estimates (Ash et al 2022).

Two previous studies had tried to decode the waggle dance in a similar way, but they compared only two single sites. Garbuzov et al (2015) found a preference for urban over rural land by the bees, whereas Sponsler et al (2017) found the opposite (Ash et al 2022).

4.8. BIRD NUMBERS

Callaghan et al (2021) combined data from studies using the app "eBird", via which individuals can submit bird sightings. The overall pattern was that "across the globe there are many species with small populations isolated in niche habitats and relatively few species that have managed to expand over a wide territory and grow their population into the hundreds of millions or billions" (Moskowitz 2021 p80). The most abundant of nearly 10 000 species were the house sparrow, European starling, ring-billed gull, and barn swallow (Moskowitz 2021).

It was estimated that around 10% of species had populations of less than five thousand individuals (eg: Great Spotted Kiwi 377 individuals (figure 4.5); Malaita Fantail fewer than 100 individuals) (Moskowitz 2021).

(

Source: Szilas; in public domain)

Figure 4.5 - Stuffed Great Spotted Kiwis in a museum in New Zealand.

4.9. OWLS AND CHANGE

Fragmentation of rural habitats occurs as cities expand, and the ability of a species to adapt is key to survival. Referring to bird species, Pagaldai et al (2021) observed that "sensitive" species remain on the outskirts of the city while "urban species", like raptors, survive within the city.

Pagaldai et al (2021) studied an example of the latter, the tawny owl (Strix aluco) in the Basque Country, in northern Spain in 2018.

Sixty-five 25 km^2 areas known as "Universal Transverse Mercator" (UTM) squares were randomly selected and over seven months regular surveys of the owls were made by twenty-four observers (n = 527 survey points). At night calls were played and the responses were counted.

In total, 680 owls were detected, with responses at 70% of the survey points (with 1-5 individuals per survey point).

Most owls were found in the medium forested UTM squares, while in urban ones, these birds preferred smaller urban towns to cities.

In a study of Tawny owls (Strix aluco) in Israel, Comay et al (2022) found that climate change had a greater impact than rural development on these birds. Tawny owls living in Israel are at the southern edge of their distribution, and this could increase their sensitivity to temperature and rainfall changes.

Data were collected in the Upper Galilee area between 1987 and 1998. Recordings of calls were played in order to produce a response, and thus to count the numbers in late winter and early spring each year. Nesting boxes and sites were also visited in the nesting season (March-July), and information gathered about the parents and the chicks.

A small number of nests (n = 105) were studied in detail, and three developmental milestones recorded - "fledging" (the presence of a chick outside the nest), "nest leaving" (the chick is more than 150 m away from the nest), and "adolescence" (when the parents cease feeding).

Higher maximum temperature in March-May had a negative effect on number of fledglings. The owls preferred relatively cool, rainy, and wooded areas. "Tawny Owls raised more hatchlings in pine forests, especially when spring temperatures were moderate and following rainy winters" (Comay et al 2022 p1).

4.10. TRESPASS CANNABIS CULTIVATION AND WILDLIFE

Illegal cannabis cultivation on public lands ("trespass cultivation") is a problem in California and Southern Oregon for wildlife "due to the rampant use of pesticides, habitat destruction, and water diversions associated with trespass grow sites" (Wengert et al 2021 p1). Two endangered species are particularly badly hit - the fisher (Pekania pennanti) (figure 4.6), and the northern spotted owl (Strix occidentalis caurina) (figure 4.7) - while the Pacific marten (Martes caurina) is also at risk. "All three sensitive forest species consume prey at risk of contamination with anti-coagulant rodenticides and other toxic pesticides within cultivation sites" (Wengert et al 2021 p2).

Wengert et al (2021) explained: "Eradication and reclamation (elimination of trash, infra-structure, and chemicals), followed by ecological restoration, are necessary to mitigate any threats to the environment, wildlife and other resources from trespass cannabis cultivation sites. However, financial and logistical challenges limit the ability of law enforcement to locate trespass grow sites using aerial reconnaissance or other methods, and discovery of all sites is infeasible" (p2). These researchers attempted to model where trespass cultivation might occur in Southern Oregon and California using data on sites found by law enforcement agencies between 2007 and 2014.

The model predicted forested regions in low to mid-elevation forests (800 -1600 metres above sea level), on moderate slopes (30-60% inclination), and close to water (less than 200 metres) would be chosen. "Somewhat paradoxically, results also suggest that growers either prefer sites inside of recently disturbed vegetation (especially those burned 8–12 years prior to cultivation) or well outside of (>500 metres from) recent disturbance. Siting within recently burned areas likely reflects a preference for post-fire vegetation conditions (eg: sufficient sunlight for cannabis growth but with some brushy understory to obscure plots)" (Wengert et al 2021 p12). These types of sites are likely to overlap with up to half of the habitats of the three sensitive species mentioned (figure 4.8).

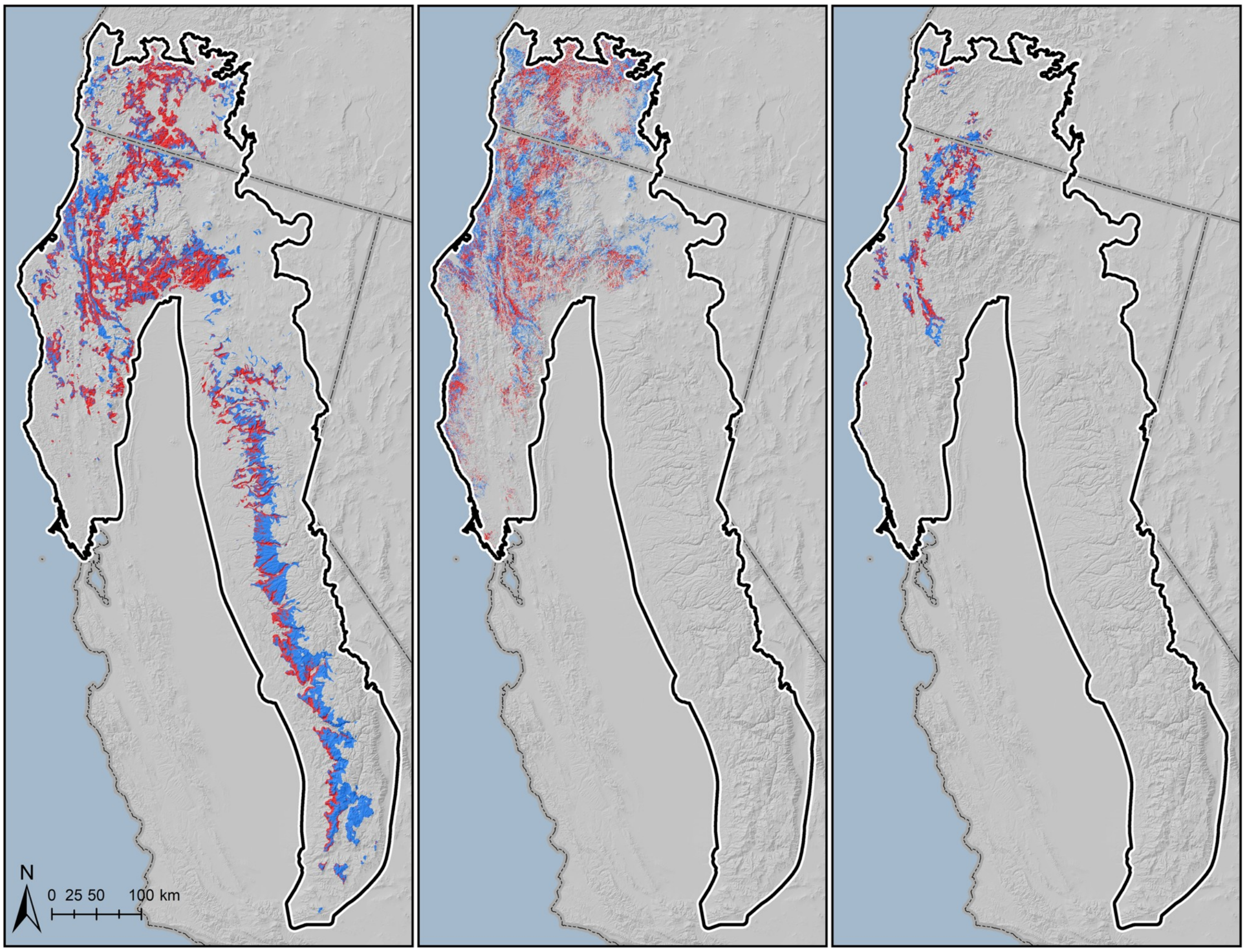
4.10.1. Figures

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

Figure 4.6 - Fisher.

(Source: US Forest Service - Pacific Northwest Region; public domain)

Figure 4.7 - Spotted owl.



(Source: Wengert et al 2021 figure 5)

Figure 4.8 - Overlap of moderate to high trespass cannabis cultivation site likelihood (red) with modelled habitat for Pacific fisher (left), northern spotted owl (centre) and Humboldt marten (right).

4.11. REFERENCES

Ash, E.S et al (2022) Dancing bees evaluate central urban forage resources as superior to agricultural land Journal of Applied Ecology 59, 79-88

Boersma, J et al (2021) Wildfire affects expression of male sexual plumage through suppressed testosterone circulation in a tropical songbird Journal of Avian Biology 52, 9, e02757

Callaghan, C.T et al (2021) Global abundance estimates for 9700 bird species Proceedings of the National Academy of Sciences, USA 118, 21, e2023170118

Cleary, A.C et al (2021) 50 000 years of ice and seals: Impacts of the Last Glacial Maximum on Antarctic fur seals Ecology and

Evolution 11, 14003-14011

Coggan, N.V et al (2018) A global database and "state of the field" review of research into ecosystem engineering by land animals Journal of Animal Ecology 87, 4, 974-994

Comay, O et al (2022) In its southern edge of distribution, the Tawny owl (Strix aluco) is more sensitive to extreme temperatures than to rural development Animals 12, 641

de Lima, H.P et al (2022) Temporary storage along swarm columns of army ants: An adaptive strategy for successful raiding Biology Letters 18, 20210440

Duarte, C.M et al (2020) Rebuilding marine life Nature 580, 39-51

Garbuzov, M et al (2015) Eating locally: Dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area Urban Ecology 18, 411-418

Gurney, G.G et al (2021) Biodiversity needs every tool in the box: Use OECMs Nature 595, 646-649

Hindell, M.A et al (2020) Tracking of marine predators to protect Southern Ocean ecosystems Nature 580, 87-92

Lundgren, E.J et al (2021) Equids engineer desert water availability Science 372, 491-495

Martin, A et al (2020) Study the twilight zone before it is too late Nature 580, 26-28

McCallum, E.S et al (2014) Seasonal plasticity in telencephalon mass of a benthic fish Journal of Fish Biology 85, 1785-1792

Moskowitz, C (2021) Counting birds Scientific American August, p80

Pagaldai, N et al (2021) Colonisation of urban habitats: Tawny owl abundance is conditioned by urbanisation structure Animals 11, 2954

Purser, A et al (2022) A vast icefish breeding colony discovered in the Antarctic Current Biology 32, 4, 842-850

Sequeira, A.M.M (2020) Predators on track for ocean protection Nature 580, 34-35

Sheard, J.K et al (2021) Long-term trends in the occupancy of ants revealed through use of multi-sourced datasets Biology Letters 17, 20210240

Sponsler, D.B et al (2017) Spatial and taxonomic patterns of honey bee foraging: A choice test between urban and agricultural landscapes Journal of Urban Ecology 3, 1, juw008

Versteeg, E et al (2021) Seasonal variation of brain size in a freshwater top predator Authorea

(https://www.authorea.com/doi/full/10.22541/au.162312317.76022973)

von Frisch, K (1967) The Dance Language and Orientation of Bees Cambridge, MA: Belknap Press of Harvard University Press

Wagner, T.C et al (2021) Rolling pits of Hartmann's mountain zebra (Zebra equus hartmannae) increase vegetation diversity and landscape heterogeneity in the Pre-Namib Ecology and Evolution 11, 13036-13051

Wengert, G.M et al (2021) Distribution of trespass cannabis cultivation and its risk to sensitive forest predators in California and Southern Oregon PLoS ONE 16, 9, e0256273 (Freely available at https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0256273)

5. GROUP BEHAVIOURS

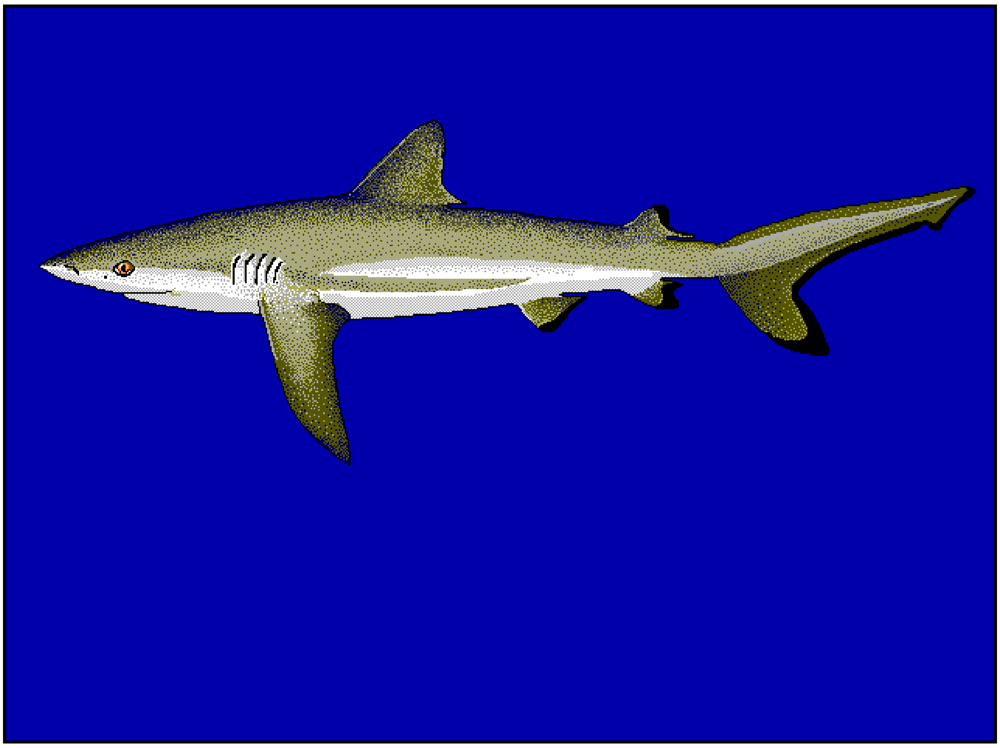
5.1. SHARKS

Animals in groups can "exhibit fission-fusion dynamics, where individuals split from (fission) and re-join (fusion) other group members" (Papastamatiou et al 2020 p1). "Central place foragers" (CPF) show such behaviour. This involves "animals making excursions individually or in smaller groups to/from the larger group at the central place. For example, seals and seabirds reside in groups or colonies on land but head offshore to forage in much smaller groups. In most cases, the central place is the location of a nest, shelter or haul-out site which explains loyalty and fidelity to the central place" (Papastamatiou et al 2020 p2).

This suggests that reproduction drives the motivation of CPF. But social information-sharing may also be a motive. This includes "local enhancement (where animals can detect other individuals foraging and can simultaneously forage and observe conspecifics), recruitment (an individual 'recruits' others to a patch, with foraging success increasing with group size, ie: the recruitment hypothesis) and public information (where uninformed individuals follow informed individuals to prey patches)" (Papastamatiou et al 2020 p2). Models of CPF suggest that the social information motive only applies when prey is unpredictable and available for limited times (Papastamatiou et al 2020).

Sharks, for example, are CPF where there is no nest or shelter, and they "have no obvious need to return to a central place" (Papastamatiou et al 2020 p2). Tropical reef shark form groups during the day, and disperse alone or in small groups to forage at night. The motivation as CPF is unknown in this species (Papastamatiou et al 2020).

Focusing on grey reef sharks (Carcharhinus amblyrhynchos) (figure 5.1) at Palmyra Atoll in the Central Pacific Ocean, Papastamatiou et al (2020) investigated CPF. Forty-one individuals were tagged and tracked for up to four years. Group membership was defined as within one metre proximity of a conspecific.



(Drawing by Robbie.N. Ceda at http://www.fishbase.org/; in public domain)

Figure 5.1 - Drawing of grey reef shark.

The reproductive success explanation of CPF was dismissed as sharks do not display any parental care, and so the social information explanation was accepted. Based on the data collected on movements and aggregations, which showed stability over time (ie: the same individuals associating), simulations were created suggesting the CPF will outperform the non-CPF. Social information is important because the schools of prey fishes are unpredictable. It was felt that local enhancement social information was particularly supported by the data and modelling.

5.2. TERMITES

Providing shelter for oneself can be expensive, and so co-habiting (or "squatting") with others is a possibility. This is seen in termite nests where a host (nest builder) shares with another species of termite (called "inquilines") (Hugo et al 2020).

Termites are notoriously aggressive towards nest invaders, so how do inquilines survive? There are a number of possible answers, including (Hugo et al 2020):

a) Chemical:

i) Inquiline termites change their chemical signature to that of the host or similar enough to become undetectable to the hosts.

ii) inquilines intercept chemical signals of the host and use them to avoid encounters.

b) Behaviour:

i) Inquilines avoid host crowded areas.

ii) Inquilines build own galleries and areas in the colony.

iii) Inquilines have different dietary requirements to hosts, which avoids contact and competition for resources.

In the main, these strategies all mean avoiding contact with the host species.

Hugo et al (2020) studied the host termite, Constrictotermes cyphergaster, and an obligate inquiline termite, Inquilinitermes microcerus, in 27 nests in Brazil (that were transferred to the laboratory).

The two species in groups of fifteen were placed in closed or open arenas. The former had no exit, thereby forcing the inqulines to interact with the hosts. Twenty five-minute videotaped experiments were performed, and the behaviour of each individual was categorised (eg: moving; resting; aggression).

Hosts were more likely to be aggressive when encountering inquilines, while inquilines did not retaliate, but rather evaded the attackers, and used other strategies to avoid contact (eg: resting).

Hugo et al (2020) described "an unexpected response among inquiline workers: When threatened by hosts, inquiline workers deposited faecal pellets always toward the direction from which they suffered threats. Rather than usual defecations, this behaviour seemed to be elicited by host aggressions as follows: When receiving attacks from backwards, individuals immediately placed faecal pellets in front of the head of aggressors and escaped forward. When threats came from any other direction, however, a different response was triggered: Before defaecation, individuals first adjusted their posture to allow the faecal pellets to be dropped right in front of the aggressor's head. Only after such a move, inquiline workers defecated and escaped forward" (pp8748-8749). The faeces may have a chemical repellent effect, or as a physical defence in narrow galleries.

So, in situations of being constantly surrounded by potential aggressors, inquilines use non-aggressive behaviours.

The inquiline species studied was obligate, meaning that it has no other nesting behaviour than nest invasion/sharing. "Nest invaders are not required to spend time and energy building their own home. At the same time, being nest building a demanding, costly process..., one would expect such inquiline invasions to be not strictly in the interest of hosts. In this sense, it would be reasonable to think of a scenario in which hosts would endeavour to detect inquilines, whereas inquilines would try to go unnoticed by hosts. This evasive behaviour, consistently exhibited at the individual level, confers a conflict avoiding strategy to the inquiline colony as a whole. Under the effect of such driving forces, it is likely that an evolutionary arms race between species would take place..., leading hosts and inquilines to reach well-adjusted behavioural profiles. In doing so, each species would become highly specialised in dealing with its co-habiting neighbour" (Hugo et al 2020 p8751). Put simply, a balance based on conflict avoidance and management has been reached (in evolutionary terms).

5.3. COCKROACHES

Eusociality or "full sociality" is "a social system characterised by co-operative brood care, differentiation into castes and a complete generational overlap... It results into loss of individuality and so called super-organismal structure of animal units" (Hinkelman et al 2020 p2). It is common in termites and ants, but not cockroaches usually. Hinkelman et al (2020) reported observations of the cockroach genus Melyroidea that appear as exceptions.

A nest was found in 2017 in the cloud forests on the Eastern slopes of the Andes (in Peru, Ecuador and Brazil) by the researchers. An endoscope was inserted into the nest to monitor activity within. Other nests and colonies in the area were subsequently observed.

A new species was reported, Melyroidea ecuadoriana, and the eusocial behaviour of Melyroidea magnifica

(Blister beetle mimic) was observed. Another species, undocumented at this time, was also photographed. The problem is that little is known about cockroaches in this area, of which there are approximately 200 species (Hinkelman et al 2020). The researchers could not confirm beyond doubt that eusociality was present in these cockroaches. For example, a large white M. magnifica seen in the nest was assumed to be a "queen", but it was not known if she was the sole breeding individual in the colony (a key requirement of eusociality).

Cockroaches as a generalisation feed on dead organisms (detritivory), but these species had diets of fungi (fungivory) and/or algae (algaevory). So, eusociality could have evolved with the diet shift (Hinkelman et al 2020).

It is also possible that there are "various degrees of sociality" (Hinkelman et al 2020 p15).

5.4. REFERENCES

Hinkelman, J et al (2020) Neotropical Melyroidea group cockroaches reveal various degrees of (eu)sociality The Science of Nature 107, 39

Hugo, H et al (2020) Non-aggressive behaviour: A strategy employed by an obligate nest invader to avoid conflict with its host species Ecology and Evolution 10, 8741-8754

Papastamatiou, Y.P et al (2020) Multi-year social stability and social information use in reef sharks with diel fission-fusion dynamics Proceedings of the Royal Society B 287, 20201063