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Humans and Others

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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/.

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1. HOMO SAPIENS

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1.1. STATE OF KNOWLEDGE

Lawton (2019) summed up the view on the evolution of humanity at the beginning of the 21st century: "Homo sapiens evolved in eastern Africa about 150 000 years ago, became capable of modern behaviour some 60 000 years ago (YA) and then swept out of Africa to colonise the world, completely replacing any archaic humans they encountered" (p34). This is known as the "recent out-of-Africa paradigm" (Lawton 2019).

But discoveries in the last twenty years have challenged this view. The main points of issue are:

i) The date and place of evolution of Homo sapiens - An idea called "African multi-regionalism" has emerged, where humanity is seen as evolving more widely in Africa and elsewhere, and at an earlier time (500 - 300 000 YA) (Lawton 2019) (table 1) [1].

Name	Dated at	Found
Jebel Irhoud	315 000 YA	Morocco
Florisbad *	260 000 YA	Southern Africa
Omo **	200 000 YA	Ethiopia
Herto ***	160 000 YA	Ethiopia
Laetoli ****	120 000 YA	Tanzania

(* Looks similar to modern humans - eg: prominent chin, spherical brain case, and flat face compared to extinct ancestors;
** Modern and archaic features;
*** Mix features but distinct from Omo;
**** "More modern but more archaic-looking" (Lawton 2019))

(Source: Lawton 2019)

Table 1.1 - Key fossil skull finds in the evolution of Homo sapiens [2].

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[1] In terms of early humans out of Africa, Stewart et al (2020) recently reported footprints in the Nefud Desert, Saudi Arabia. Dating of the adjacent sediments suggested early humans here earlier than previously thought (over 100 000 YA). Fossils of Homo Sapiens have been recorded in Europe 210 - 180 000, but previously in Arabia 85 000 YA (Stewart et al 2020).

[2] The dating of fossils is key, including the age of sediments around the find. Radiocarbon dating is commonly used, and it involves the speed of decay of certain carbon isotopes after death. Other techniques are based on chemical processes like the uptake of uranium from the soil and its decay (U-series dating) (Lawton 2019).

ii) The intellectual development at an earlier date - Evidence of sophisticated stone tools earlier than 60 000 YA, and among other hominins.

iii) Homo sapiens replaced other hominins - Barras (2016) noted that the view in 2010 was that "one feature united the ancient human species that once walked the Earth: all were well and truly extinct" (p38). But DNA evidence shows now that these ancestors have left a genetic legacy in humans.

This DNA manifests itself in different ways, like red hair and freckles, susceptibility to hay fever and common allergies, or small increased risks of depression, heart attack, and nicotine addiction (all linked to Neanderthals) (Barras 2016).

This DNA exists because of mating between humans and others to produce "hybrid" offspring. Interbreeding may have ended only 9000 years ago, according to statistical analysis of the human genome (Barras 2016) (table 2) [3].

- Three genomes have been mapped for ancient ancestors (known as the DAV genome) (Skov et al 2020):
- D - Denisovan individual (Meyer et al 2012).
- A - Neanderthal from Altai Mountains (central Asia) (Prufer et al 2014).
- V - Neanderthal from Vindija Cave (modern-day Croatia) (Prufer et al 2017).

Table 1.2 - Source of ancient hominid DNA.

So, "groups of more-or-less modern humans, evolving semi-independently", while isolated populations of mosaics of archaic and modern features held out to relatively recently (eg: 14 000 YA) (Lawton 2019).

Traditionally, a species is defined as its ability to breed between members and produce fertile offspring (Douglas 2019) [4]. Yet coyotes and grey wolves (separate

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[3] Genetic admixture from Neanderthals into Homo sapiens (around 1-2% of all non-African human DNA today) around 80 - 40 000 YA (Schierup 2020).

But the limited number of gene sequenced Neanderthals from bones suggested a gene flow from Homo sapiens 300 - 200 000 YA (Schierup 2020). Petr et al (2020) sequenced DNA from bones of male Neanderthals and Denisovans finding support for this gene flow. Schierup (2020) explained that this new study "unequivocally shows that both male and female H. sapiens contributed to gene flow, suggesting that both H. sapiens and Neanderthal populations accepted children of mixed heritage" (p1566).

[4] This is one of over thirty definitions of species (eg: lifestyle; form; shared genetically encoded characteristics). "Biology is messy, and doesn't tend to our desire for clear classifications" (Douglas 2019 p39).

species) can breed to produce another species, red wolf (appendix 1A). If Homo sapiens were breeding with other hominins, then the term "clade" for Homo sapiens may be better - "a group of organisms of various taxonomic groups, descended from a common ancestor and sharing may factors, but also with a lot of physical variation" (Lawton 2019 p39).

But there appears to be no common ancestor of humans and Neanderthals (Lawton 2019).

1.2. PLACE OF ORIGIN

Using genetic analysis of mitochondrial DNA of modern individuals in southern African (eg: Khoisan people), Chan et al (2019) suggested the origin of Homo sapiens in wetlands in modern-day Botswana, Namibia and Zimbabwe (ie: south of the Zambesi river) 200 000 YA.

But critics argued that this study missed lineages of humans elsewhere in Africa because of the focus on a specific area (Sample 2019).

1.3. APPENDIX 1A - HYBRIDISATION

"Hybridisation" is the inter-breeding between similar species [5], and it is thought to be widespread, but random. "Although hybridisation is often considered deleterious, it is increasingly recognised as potentially fitness enhancing if mates of one's own species (ie: conspecifics) are limited or if hybrids are better adapted to their environment than pure-species types" (Chen and Pfennig 2020a p1377).

This opens up the possibility of sexual selection between species, which Chen and Pfennig (2020a) investigated with female plains spadefoot toads (Spea bombifrons) (figure 1.1) in south-west USA, which can mate with Mexican spadefoot toads (Spea multiplicata) (figure 1.2).

Hybrid tadpoles develop faster than pure plains spadefoot toads, which is an advantage in transitory

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[5] Such a possibility "could affect the evolution and distribution of sexual signals, local mate competition, and even the extent to which species do or do not diverge where they co-occur" (Chen and Pfennig 2020a p1379).

(Source: Veronica Kelly, USFWSmidwest; in public domain)

Figure 1.1 - Plains spadefoot toad.

desert ponds that dry up quickly. "Consequently, female S. bombifrons have evolved mate preferences for S. multiplicata males but only in shallow, ephemeral ponds; when a pond is deep and likely to last long enough for S. bombifrons tadpoles to successfully metamorphose, S. bombifrons females prefer males of their own species" (Chen and Pfennig 2020a p1377) [6].

Chen and Pfenning (2020a) showed this difference in experiments where female plains spadefoot toads were offered Mexican spadefoot toad males of varying quality

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[6] This female preference appears to have evolved in sympatry (ie: environments where hybridisation occurs), but not in allopatry (ie: environments where hybridisation does not occur because the other species is not present) (Chen and Pfennig 2020a).

(Source: Sarah Beckwith; in public domain)

Figure 1.2 - Mexican spadefoot toad.

based on calls. "Tadpoles resulting from S. bombifrons females crossed with S. multiplicata males had the highest fitness when their fathers had calls with slow pulse rates" (Chen and Pfennig 2020a p1377).

The survival of fifty hybrid tadpoles was monitored for twelve days. Braun et al (2020) criticised this measure of fitness: "Complete fitness estimates require following the fate of offspring from zygote until reproduction and ideally until death" (p1) Chen and Pfennig (2020b) responded that early growth is most crucial because of the quick drying of desert pools where the tadpoles lived.

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2. HOMININS

2.1. Early hominins
2.2. Extinction of Neanderthals
2.3. Homo erectus
2.4. Dating of fossils
2.5. References

2.1. EARLY HOMININS

One of the earliest hominins, Australopithecus africanus, lived between 3 million years ago (MYA) and 2 MYA. They were believed to eat fruits, leaves, grasses, and roots based on the physical appearance of the skull and jaw (Joannes-Boyau et al 2019).

They lived in Southern Africa where seasonal variations in food availability occurred. "This cyclical rhythm of dry open grassland in winter and wet blooming woodland in summer prompted mammals to adapt either by undertaking long annual migrations to more clement regions, or, to adapt to seasonal food consumption, including the use of fall-back resources (those with poor nutritional values eaten only when preferred foods are scarce or unavailable). This climatic cycle has consequences on the physiological (eg: nursing, reproduction and infant development) and ecological behaviour (eg: diet, grouping of individuals, territory size) of endemic species, particularly to non-migrating individuals" (Joannes-Boyau et al 2019 p112).

Joannes-Boyau et al (2019) chemically analysed the fossilised teeth of infants of this species. For example, barium concentrations increase with absorption from mother's milk and decline with weaning. The researchers concluded that "Australopithecus africanus had a short period (not exceeding a year), which is a very different sequence to extant great apes and instead has a timing comparable with modern Homo species. Yet, since nursing and seasonal dietary banding cannot be precisely disentangled, it remains possible that the species retained a lengthy weaning sequence well into an advanced age of the offspring to overcome seasonal food shortage, similar to modern day great apes. Our results identified important dietary cycles and physiological adaptations in response to food access, which would have had important repercussions on social structures and ecological behaviours adopted by A. africanus groups. These adaptations in response to seasonal variability and resource scarcity, would have extracted a toll on the resilience to other environmental pressures, thus possibly playing a role in the disappearance of the genus from the fossil record at about 2 MYA" (Joannes-Boyau et al 2019 p114).

Australopithecus anamensis (4-2 MYA) is viewed as the ancestor species of A. africanus [7], which in turn is "widely thought to have been our own ancestor" (Marshall 2019a p15). But new finds (eg: Saylor et al 2019) suggest that A. afarensis as older than A. anamensis, and A. anamensis split into two (a continuing A. anamensis for a while, and A. afarensis) (Marshall 2019a).

2.2. EXTINCTION OF NEANDERTHALS

One theory is that Neanderthals became extinct because Homo sapiens had a direct or indirect impact on them (Marshall 2019b).

At approximately 60 - 40 000 YA the populations of Neanderthals in Europe were small when confronted by Homo sapiens (or anatomically modern humans; AMHs) from Africa. Vaesen et al (2019) place importance of this fact rather than other explanations for the extinction of Neanderthals, which include climate change, epidemics, and "a superiority of AMHs over Neanderthals in competing for the same resources" (p1).

One estimate is that the total number of Neanderthals was "no more than 3000 - 3900 individuals" (p2) by 40 000 YA. Other estimates are larger, but, whatever the size, the "global population was sub-divided in very small and highly isolated local populations" (Vaesen et al 2019 p2).

Vaesen et al (2019) outlined three factors that interacted in Neanderthal extinction:

i) Inbreeding, which could have reduced Neanderthal genetic fitness by nearly half compared to humans (eg: Harris and Nielsen 2016).

ii) "Allee effects" - the relationship between individual fitness and population size (eg: a problem with finding a mate in a small population). As well as this problem, there would be "low availability of helpers in co-operative hunting, defending kills from kleptoparasites, and allo-parenting" (Vaesen et al 2019 p2).

iii) Random annual fluctuations in births, deaths and sex ratio (ie: stochastic factors), which are "more likely to place smaller populations on a trajectory towards extinction than bigger ones" (Vaesen et al 2019

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[7] By a process of anagenesis, where one species evolves into another species.

p2).

Vaesen et al (2019) modelled the three factors for the survival of a population. Key variables were the average number of female offspring per year, and the yearly survival of females.

Vaesen et al (2019) summed up: "Our results indicate that the disappearance of Neanderthals might have resided in the smallness of their population(s) alone: even if they had been identical to modern humans in their cognitive, social and cultural traits, and even in the absence of inter-specific competition, Neanderthals faced a considerable risk of extinction. Furthermore, we suggest that if modern humans contributed to the demise of Neanderthals, that contribution might have had nothing to do with resource competition, but rather with how the incoming populations geographically restructured the resident populations, in a way that reinforced Allee effects, and the effects of inbreeding and stochasticity" (p1).

2.3. HOMO ERECTUS

Homo erectus, "our most likely direct ancestor", survived for 1.5 million years (Anton 2020). During this time, there was overlap between this species, and the genera Pranthropus and Australopithecus. The extent of the overlap is the issue. The contemporaneity of these genera is shown by recent skull finds at ancient caves (Drimolen) in South Africa (Herries et al 2020) [8].

Around 2 MYA there was a variety of Homo species (including Homo habilus and Homo rudolfensis) [9], with Homo erectus appearing in Kenya 1.87 MYA. Paranthropus aethiopicus and Paranthropus boisei appeared 2.7 and 2.3 MYA respectively in East Africa, while Paranthropus robustus was in South Africa by 1.8 MYA. All these species overlapped for about half a million years (Anton 2020) (figure 2.1).

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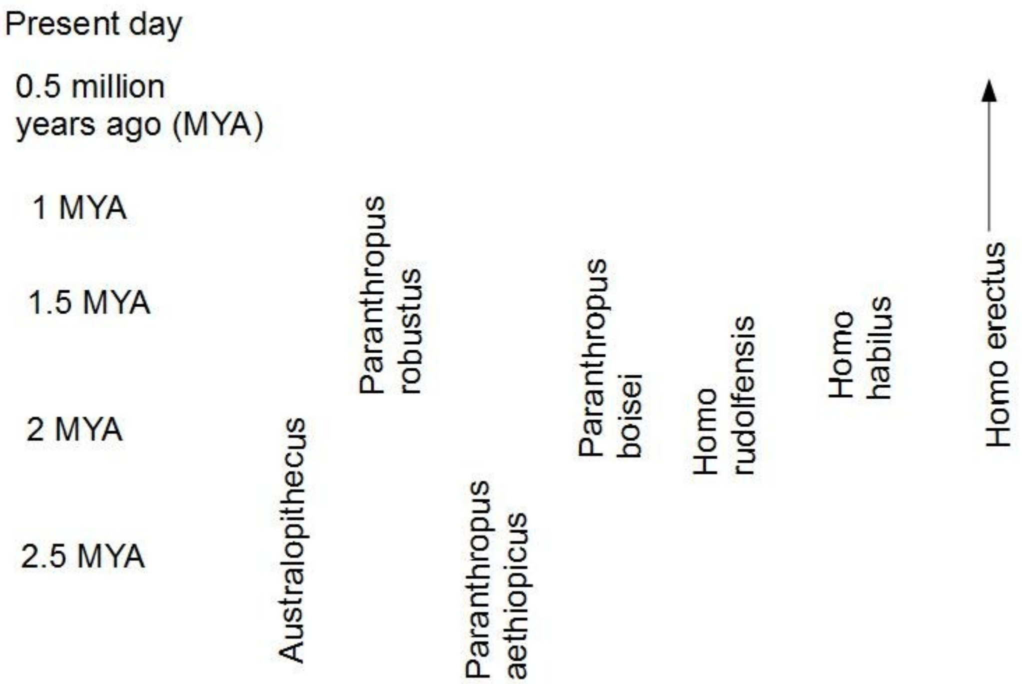
[8] The dating of fossils also involves the dating of the environment where the items were found (eg: rocks, fauna remains).

[9] The earliest Homo species is dated at 2.8 MYA (Anton 2020).



(After figure p 35 Anton 2020)

Figure 2.1 - Overlap between different species of archaic human species.

Homo erectus can be seen as distinct from other species in that it was "the first species to leave the African continent. In fact, almost as soon as they arose, H. erectus appeared outside of Africa at the site of Dmanisi in the Republic of Georgia. Over the next nearly 2 million years, H. erectus occupied a variety of different habitats and contexts before going extinct well after 0.5 million years ago on present-day Java. The initial moves in H. erectus dispersal were so quick that researchers have questioned whether H. erectus might instead have originated in Asia" (Anton 2020 p35).

2.4. DATING OF FOSSILS

The understanding of hominins is also made more difficult when fossil finds are reclassified and disputed as in a skull from Broken Hill, Zambia. Originally found in 1921 during metal ore mining, it was designated as Homo rhodesiensis (Woodward 1921) [10]. Later, it was reclassified as Homo heidelbergensis (eg: Stringer 1983).

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[10] It is possible that the skull was found in 1908 (Grun et al 2020).

Grun et al (2020) used the latest dating methods recently.

They explained the situation: "Because of poor provenance, the Broken Hill material has been difficult to date, and the site has since been completely destroyed by quarrying. Previous assessments had placed the whole assemblage of human fossils, fauna and artefacts in the late Pleistocene epoch. More recently, faunal comparisons made with sites such as Olduvai and Elandsfontein have suggested a Middle Pleistocene age, perhaps as old as 500 thousand years (kyr). However, the limited (and poorly associated) archaeological materials have consistently been attributed to the later Pleistocene/early Middle Stone Age" (Grun et al 2020 p373) [11] [12].

Grun et al (2020) admitted that dating was difficult because of the provenance, but estimated 300 000 YA (with a range of 25 000 years either way).

As to the species, "the skull shows no direct traits characteristic of anatomically modern humans" (Grun et al 2020 p375). However, what the skull showed for Grun et al (2020) was the presence of different species at the same time. They stated that "just as Eurasia in the later Middle Pleistocene contained the multiple evolving lineages of H. neanderthalensis, Denisovans, H. floresiensis, H. luzonensis and perhaps also H. heidelbergensis and H. erectus, different human lineages and/or species also co-existed across Africa. As well as the recently identified H. naledi, these included late H. heidelbergensis/H. rhodesiensis as represented by the Broken Hill skull, and early H. sapiens, as represented by fossils such as those from Jebel Irhoud, Florisbad and Guomde" (Grun et al 2020 p375) [13].

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[11] The Pleistocene epoch goes from 2.5 MYA to 11 700 YA, with the Middle period being 700 000 to 200 000 YA, and the Late/Upper period after that. The Stone Age began 1 MYA (Burenhult 2003).

[12] Olduvai in Tanzania, and Elandsfontein in the Western Cape, South Africa.

[13] Jebel Irhoud in Morocco, Florisbad in South Africa, and Guomde in Kenya.

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3. TOOL USE AND COGNITION

3.1. Technition
3.2. Appendix 3A - Evolution of self-control
3.3. References

3.1. TECHNITION

Osiurak et al (2020) introduced the term "technition" to describe the study of the "neurocognitive bases of the human technical mind" (ie: tool use and "other forms of technologies, including constructions") [14].

Traditionally, early hominin and human tool use is seen as a response to environmental pressures to survive. But Osiurak et al (2020) challenged this view: "The question is why we keep on making tools that have no apparent interest in survival (eg: TV remote). Instead of focusing on external incentives, a more Lorentzian view is to consider that we use tools because our technical-reasoning skills lead us to generate our own physical problems in an instinctive way... This could explain the presence of a human preference for using tools even when they are less effective than doing without them" (p890).

Osiurak et al (2020) argued that we have "perhaps uniquely human neurocognitive skills" [15], namely, "technical reasoning" [16], which leads to the generation of technical solutions to solve problems. The authors explained further: "Technical reasoning is a specific kind of reasoning that is directed toward the physical world. In this respect, it must not be confounded with other forms of non-verbal reasoning, such as fluid cognition. More specifically, fluid cognition allows humans to develop logical thinking that does not need a precise understanding of physical constraints... Evidence has shown dissociations between fluid cognition and technical-reasoning skills both at a behavioural level... and at a neural level... In addition, technical reasoning is not restricted to the spatial dimension of the physical world. To master the mechanical action 'percussion', for instance, requires much more than simply matching two (or more) objects spatially. One also needs to understand other properties (eg: rigidity, weight) that go beyond the mere spatial dimension" (Osiurak et al 2020 p893).

Osiurak et al (2020) also saw "technical reasoning"

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[14] Osiurak and Heinke (2018) called the intelligence behind tools "intoolligence".

[15] Green and Spikins (2020) linked tool use to the evolution of self-control (appendix 3A).

[16] It is linked to the area "PF" in the left inferior parietal lobe (Osiurak et al 2020).

in "secondary tool use" ("the ability to use one tool to create another").

These authors also emphasised the importance of "tool-saving". This is "cognitively demanding because it imposes to plan an action (ie: put a tool aside) for a potential future need rather than a current one. In this way, tool saving is at the crossroads of tool use and what is called future planning" (Osiurak et al 2020 p891).

To end their article, Osiurak et al (2020) quoted Wynn et al (2017): "The human mind is not a single cognitive phenomenon. It consists of many interconnected networks, each of which has its own evolutionary history. One such system that has been underappreciated in evolutionary studies, but which governs many activities in the modern world, is skilled technical cognition. Unfortunately, this kind of thinking is not held in high regard in academic discourse where verbal and mathematical thinking are the primary tools of scholarship. And yet, for most of human evolution, day-to-day technical thinking was almost certainly more important to the evolutionary success of our ancestors".

3.2. APPENDIX 3A - EVOLUTION OF SELF-CONTROL

Self-control is the "ability to subdue immediate impulses in order to achieve long-term goals" (Green and Spikins 2020 p117). What about its evolution?

"Self-control plays a role in collaborative practices, such as hunting and food sharing, and reciprocal altruism... All these abilities contribute to human hyper-sociality" (Green and Spikins 2020 pp117-118). So, selective pressure on early humans to live together and co-operate will be important in the explanation of the evolution of self-control.

Green and Spikins (2020) used archaeological evidence to explore the evolution of self-control. From this evidence, theories about behaviour and the underlying cognitive and neural architecture can be produced (figure 3.1). For example, the design of a stone tool suggests hours of work in crafting it, and self-control is needed to achieve such discipline and concentration.

Archaeological Object → Procedures and Knowledge to produce object → Underlying Cognition

(After Green and Spikins 2020 figure 1 p119).

Figure 3.1 - From archaeological evidence to cognition.

It is important to establish what cognitive processes are involved in self-control. These include (Green and Spikins 2020):

- Executive functions to focus attention on one thing and not another, working memory to remember the ultimate goal, and cognitive flexibility to change between tasks as required.
- Emotion regulation.

Together these abilities appear in deliberate practice needed to produce an elaborate stone axe, say. "Deliberate practice is an effortful activity directed at honing skills. It is a cognitively complex process that relies on all the executive functions... It requires that an individual maintain focus on their goal – eg: creating a better handaxe – while constantly monitoring and altering their behaviour in service of that goal. As part of this, automatic responses must be controlled and replaced with new ones" (Green and Spikins 2020 p127). Add to this planning in terms of collecting the raw materials, and "mental time-travel" to imagine the finished product.

Flint axes, for instance, are made by removing flakes of stone in a process called knapping. It is easy, particularly for the unskilled, to remove too much and the axe is useless. There would be frustration during this process that needed to be tolerated.

Putting all these ideas together, Green and Spikins (2020) distinguished five characteristics that can be seen as part of the psychological concept of self-control - deliberate practice, forward planning, time and energy investment, hierarchical processing (ie: a sequence of steps to follow), and distress or frustration tolerance (table 3.1).

Though chimpanzees, for example, can show some of these behaviours, it is only the combination of them all that produces the self-control capable of making sophisticated stone tools. Green and Spikins (2020) observed that "we can already see that, by c.500kya

Handaxe Production and Cognitive Characteristics	Aspects of Self-control
Deliberative practice with raw materials	Executive functions
Forward planning to collect raw materials	Executive functions
Time and energy investment in collecting raw materials, practice, and production	Emotion regulation and delay gratification
Hierarchical processing to follow the steps of production	Executive functions
Distress tolerance of mistakes and failures	Emotion regulation

(After Green and Spikins 2020 table 1 p132)

Table 3.1 - Aspects of self-control and handaxe production.

[around 500 000 years ago], the minimum capacity of self-control visible in the archaeological record was greater than that evidenced by other apes" (p131).

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4. LEARNING AND EVOLUTION

4.1. Life history and learning
4.2. Evolution
4.3. References

4.1. LIFE HISTORY AND LEARNING

Gopnik et al (2020) stated: "Human life history is distinctive, it is very different from the life history of even closely related species. In a remarkably short time, humans evolved an exceptionally long childhood and old age, and an unusually high level of caregiving investment, with a wide range of caregivers, including pair-bonded fathers, unrelated alloparents and post-menopausal grandmothers. This stands in contrast to our closest primate relatives. There is even fossil evidence for changes in life history during hominin evolution" (p1). "Life history" here refers to the evolution of the period of immaturity, and parental caregiving in a species, for example.

Humans differ from non-human primates in being more co-operative and collaborative, which includes the sharing of knowledge across generations. Human life history has a role in these differences (Gopnik et al 2020).

For example, Gurven et al (2020) considered the evolution of pedagogy - ie: "teaching by a more skilled individual that improves the ability of a less skilled individual, potentially at a cost to the teacher's own productivity" (Gopnik et al 2020 p3). Gurven et al (2020) outlined the conditions that favoured this idea, including elders instructing the young, and peer-tutoring among younger individuals. These characteristics go with a species that has an extended childhood in which to learn, and an extended lifespan so elders can pass their knowledge on.

Such a situation of cultural learning goes hand in hand with larger brain growth, plus more complex social networks (Richerson and Boyd 2020). "Without these larger social networks, children's big brains and long lifespans would not lead to humans' distinctive forms of cultural skills and knowledge" (Gopnik et al 2020 p4).

An extended period of immaturity demanding parental care is costly for mothers, in particular, in terms of fewer subsequent offspring. But co-operation in hominin societies including shared caring (alloparenting), and mothers can have other offspring. Hrdy and Burkart

(2020), however, described a new challenge for children. "With more adults to relate to and solicit care from, along with more 'competitor' siblings and other children at similar ages, there was social selection on children who could more effectively ingratiate themselves with adults. Young human children who could best read the minds of adults and communicate with them more effectively formed stronger relationships with them, to their advantage. This pattern of interaction in which children learn to share attention with others then transformed human social interactions and cultural learning across the board" (Gopnik et al 2020 p4).

4.2. EVOLUTION

It has been proposed that epigenetic changes inject uncertainty into gene expression which benefits the survival of the species (eg: Feinberg and Irizarry 2010). Such uncertainty means that when the environment changes, some individuals will do better than others, and the species will survive [17].

For example, food was scarce for early humans, so genes that encourage fat retention are beneficial. But in modern societies where food is plentiful, this leads to obesity. If these genes are removed from the population over generations, any future prolonged food scarcity will wipe out the population/species. A "built-in randomness generator" of epigenetics means that some individuals have the genes that accumulate fat and some do not. The former are more likely to die earlier in food plentiful societies (eg: from non-communicable diseases), but they are an "insurance policy" for the population/species against the return to food scarcity (Nicholls 2011).

Experimental evidence with non-human animals that are genetically identical and kept in identical conditions find variation between the individuals (eg: marbled crayfish; mice) (Nicholls 2011).

So, "what evolution has selected for is not epigenetic traits, but a genetically coded mechanism for producing epigenetic variation. This might produce variation completely randomly or in response to environmental factors, or both" (Nicholls 2011 p31).

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[17] There is often the belief that evolution is "about climbing a ladder of ever-increasing biological sophistication", but the reality is "usually much less grandiose" (Lawton 2019). "Evolution is changed gene frequency in populations" (Richard Dawkins in Lawton 2019). But after many generations, if these gene frequencies perpetuate because they give an organism a better chance of survival and reproduction, then adaptation by natural selection has occurred (Lawton 2019).

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5. ART, RITUALS AND SOCIAL LIFE

- 5.1. Art
- 5.2. Rituals
  - 5.2.1. Primates
  - 5.2.2. Sequence learning
  - 5.2.3. Cultural evolution
- 5.3. Social life
  - 5.3.1. Empathy
- 5.4. References

5.1. ART

One way to assess the cognitive ability of ancestors is through cave paintings. Figurative paintings showing human-like figures hunting, for example, is evidence of storytelling, while half animal/half human figures ("therianthropes") suggest an ability to conceive things that do not exist in reality (ie: imagination) (George 2019).

Recently, Aubert et al (2019) reported the discovery of such cave paintings in Indonesia dated at 43 900 YA, which is much earlier than previously thought (George 2019). But it is not known "what type of human" made them (George 2019).

5.2. RITUALS

Rituals are "universal patterns of human culture" involving "socially stipulated, conventional behaviours" (Legare and Nielsen 2020 p1). Legare and Nielsen (2020) explained that they are "(i) pre-defined sequences of action characterised by rigidity, formality and repetition, which is (ii) embedded in systems of meaning and symbolism, and which (iii) contains non-instrumental elements that are causally opaque and goal demoted" (pp1-2) [18].

What is their function in evolutionary terms? The answers include their role in the transmission of information within a social group (horizontal transmission) and between generations (vertical transmission), or in signalling an individual's

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[18] "Causal opacity" refers to the causal relationship between an action and an outcome being difficult for an observer to know, while "goal demotion" is "the degree to which a naive observer is challenged in intuiting the motives and goals of the agent performing the action. For example, lighting a candle in a dark room is goal apparent (a sensible and discernible goal is to illuminate the room), whereas lighting a candle in a room that is not dark is goal demoted (the purpose of this action is elusive without context — for example, it is a citronella candle that is being lit to ward off mosquitoes)" (Nielsen et al 2020 p2).

characteristics to the group. Rituals are often costly to the participants. "Willingness to incur personal cost is a powerful and reliable signal to others that you are committed to the group. For example, dutifully attending religious education classes and memorising prayers rather than seeking out more pleasurable activities signals to others that commitment to others is more important than one's entertainment" (Legare and Nielsen 2020 p2).

Other answers include that rituals "allow individuals to exert agency through action, giving the illusion of increased control that could also be related to emotional regulation and anxiety reduction and may improve perceived health" (Legare and Nielsen 2020 p4).

Del Pesco and Fischer (2020) noted rituals as crucial in the evolution of complex societies: "Due to their stylised, attention-getting and often repetitive nature, ritualised behaviours are thought to be particularly effective in regulating social relationships as these features set them apart from other behaviours, greatly reducing their ambiguity" (p1).

Nielsen et al (2020) considered ritual-like behaviour in Homo ancestors, like Neanderthals. As these species no longer exist, conclusions are drawn from fossil evidence, and only elements (i) and (iii) of Legare and Nielsen's (2020) definition of ritual can be addressed. Thus the use of ritual-like behaviour or "ritualistic actions" (Nielsen et al 2020).

Nielsen et al (2020) observed that "death-related behaviours are a good place to start" (p3). These researchers explained: "In hominins, intentional burial of the dead may date back to 400 000 BP [before present] ... although, currently, evidence is only strong for the last 150 000 years. Indeed, the earliest undisputed evidence for burial is attributed to Neanderthal contexts. These burials typically occur in inhabited cave or rock shelter sites, which have been suggested to reflect an attachment to the dead and a desire to keep them physically and metaphorically close and safe after they have died. For example, at La Ferrassie (Dordogne, France) foetuses and young children were interred, possibly with grave goods (lithics)" (Nielsen et al 2020 p3).

Note that the conclusions are drawn from known sites, and there is no way of knowing how representative these finds are. "Consequently, questions remain surrounding the intentions of — and involvement of ritual associated with — Neanderthal burial. Nonetheless, even if rituals were not a feature of Neanderthal burial, it appears that some of the socio-cognitive underpinnings of it were, including causal opacity (why keep a dead body close?) and normative action (repeated use of the same cave)" (Nielsen et al 2020 p3) [19].

Another approach is to extrapolate from the physical differences between Neanderthals and humans. For example, Neanderthals spent less time as juveniles, which would mean less time to learn from adults, and perhaps less cultural knowledge to acquire (and so less rituals). Put the other way around, "there are suggestions that the delayed maturation rate of H. sapiens in comparison with Neanderthals reflects the need to acquire more, and more diverse, social information" (Nielsen et al 2020 p4).

Group size is important and Neanderthals tended to live in low-density populations. "To be detectable in the archaeological record, rituals — whether ritualistic, individual or collective — (like any other topic subject to archaeological scrutiny) require a sufficiently large population size of individuals engaging in a particular category of behaviour, or a sufficiently large number of cases practised across time, to increase the likelihood of discovery" (Nielsen et al 2020 p5).

Nielsen et al (2020) ended: "Neanderthals were a co-operative, social, intelligent, tool-using species, which shared recent common heritage with our own lineage and likely displayed a propensity for over-imitation, and by implication, a capacity for cognition associated with ritualistic action. Yet, the evidence that rituals (larger, shared, complexes of symbolic action and beliefs) featured in their lives is neither widespread nor compelling" (p5).

5.2.1. Primates

Early hominin behaviour could be extrapolated from studying living primates. "Non-human great apes... are especially relevant as they can inform us of the potential abilities of the last common ancestor of humans and the genus Pan" (Tennie and van Schaik 2020 p1).

So, do apes show ritual behaviour? Tennie and van Schaik (2020) addressed the issue of language: "If full-blown language is necessary for rituals to be maintained, there might be little hope to find spontaneous rituals in apes (and we cannot ask the apes, either). However, single human ritual performances themselves can be language-free (imagine a solemn, silent ceremony). Therefore, while language is (at least often) a key component, it may or may not be a necessary component of

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[19] Whitehouse (2001) argued that "ritual in humans is irretrievably causally opaque, meaning that causality in human rituals is not just unknown, but actually unknowable" (Nielsen et al 2020 p2).

all rituals" (p2).

These authors dismissed courtship displays as rituals, as ritual behaviour must be copied via social learning, so not "evolved traits (or their by-products)" (Tennie and van Schaik 2020 p2).

Finally, Tennie and van Schaik (2020) produced their "minimal 'ape definition of ritual'": "Rituals consists of socially shared, symbolic feature(s) that are created via actions and/or results that require copying" (p3). However, even with this general definition, Tennie and van Schaik (2020) stated that "there is as yet no clear, unequivocal, full-blown evidence for any spontaneous minimal ritual in non-enculturated, untrained apes" (p6).

The authors dismissed claims in the media of cases of ritual behaviour, like chimpanzees throwing rocks against trees. The trees chosen had "favourable acoustic properties for display purposes and are specifically selected for stone throwing because of this [Kalan et al 2019]" (Tennie and van Schaik 2020 p4).

There is, however, the possibility of "proto-rituals" (ie: behaviours that may be symbolic), including chimpanzees placing grass blades into their ears (van Leeuwen et al 2014), or the "chimpanzee rain dance" (van Lawick-Goodall 1975) (ie: "vigorously and noisily charging as a reaction to rain (or waterfalls), but without clear chimpanzee targets"; Tennie and van Schaik 2020 p5). Both behaviours are "currently resisting an ordinary explanation" (p5), and hence the term "proto-ritual" (Tennie and van Schaik 2020).

There are researchers who see ritualised behaviours in primates. For example, Del Pesco and Fischer (2020) considered ritual greetings between male baboons living in multi-male groups: "These interactions are defined as short exchanges of non-aggressive signals between two individuals and comprise a uni- or bi-directional exchange of cohesive or affiliative signals. Notwithstanding the label 'greetings', these exchanges are not limited to departures and encounters" (p2).

There are differences between the species of baboons and they appeared to be linked to the social systems. Del Pesco and Fischer (2020) suggested that the differences provide a "glimpse" into the evolution of these greetings. They explained: "Communicative behaviours are assumed to evolve from simpler, functional behavioural patterns, such as touches and locomotion patterns. During the ritualisation process, these patterns lose their original function and become increasingly stereotyped, stylised and elaborate, resulting in unambiguous and distinctive signals. The gradient from greetings that mostly involve walking by in chacma, to incomplete and tentative greetings in yellow and olive baboons, to the highly stylised notification and more elaborate greetings in hamadryas and Guinea baboons, respectively, may indeed represent different stages of elaboration in the evolution of greeting behaviours. Whether ritualised greetings evolve, and what their form and function are, seems to depend on the social system, the species-specific evolutionary pressures acting on males and the resulting relationship dynamics" (Del Pesco and Fischer 2020 p5).

Long-term observation of white-faced capuchin monkeys (Cebus capucinus) in Costa Rica has produced some interesting findings (Perry and Smolla 2020) [20].

There are "highly idiosyncratic interaction sequences not found in the species-typical behavioural repertoire", and "these puzzling, apparently non-utilitarian social interaction sequences practised by some, but not all, capuchin monkey dyads" (Perry and Smolla 2020 p1).

Perry and Smolla (2020) called these behaviours "rituals", which they defined as "learned behavioural sequences with no obvious immediate utilitarian purpose, composed of behavioural elements repurposed from other parts of the behavioural repertoire, characterised by a high degree of attentional focus by one or both partners on the other's body and/or a ('sacred') object jointly handled by the interactants" (p1).

There was over 9000 hours of observational data on the "Flakes" group (n = 53 individuals), and 446 social interaction "rituals" seen (between 2004 and 2018). Seven elements of the rituals were distinguished including inserting a finger into a social partner's orifice (eg: mouth, ear, nostril), or inserting their finger into own orifice, and "passing an object (eg: bark, leaves, flower, stick, green fruit or hair plucked from the partner's body) back and forth from one partner to another, taking turns at the role of holding the object in hand or mouth, and extracting it (also with hands or mouth), in a very gentle 'tug-o-war'" (Perry and Smolla 2020 pp3-4). Other elements included clasping hands, putting hands over some part of the partner's face, sucking an appendage of the partner (eg: tail, finger), and "using the partner's back or belly as a drum to create loud, rhythmic noises" (Perry and Smolla 2020 p4).

Perry and Smolla (2020) speculated that "the evidence from capuchins is generally consistent with the idea that capuchin dyadic rituals serve a bond-testing function [21]. An important difference is that whereas most human rituals seem designed to promote

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[20] This population has been studied since 1990 (eg: Perry 2012).

[21] The bond-testing hypothesis (Zahavi 1977).

group-wide solidarity, capuchin (and other non-human primate) rituals seem to operate at the dyadic level" (p6). These researchers drew a parallel with ritualistic play in human children (eg: hand-clapping games or secret handshakes).

5.2.2. Sequence Learning

Sequences underlie rituals as well as tool use, for instant, and Renner et al (2020) argued that "the vicarious (but not individual) learning of novel arbitrary sequences represents a human cognitive specialisation" (p1).

Many animals can learn novel and arbitrary sequences (individual learning) usually via trial and error. Social or vicarious learning involves learning from watching another individual learn the sequence.

Renner et al (2020) devised an experiment which compared 3-5 year-old human children (n = 96) and three adult orang-utans. Three pictures of everyday objects were presented on a touchscreen, and the participants had to touch the pictures in a certain order (novel and arbitrary sequence). The correct sequence led to a reward.

In the Baseline condition, participants had to discover the sequence by trial and error, while in the Ghost condition the computer highlighted the items to show the sequence, or a human experimenter showed the correct sequence (Social condition).

Both the children and the orang-utans were similarly successful in learning the sequence with individual learning (Baseline condition), but the children were significantly better in the Social condition (vicarious learning). So, "these results show that humans, from an early age, have a facility to learn novel arbitrary sequences from others in a way that orang-utans do not" (Renner et al 2020 p7).

This fits with other research that shows that children imitate all types of sequences whether they are instrumental with an end-goal, or arbitrary (eg: Loucks et al 2017). Renner et al (2020) explained that "from an evolutionary perspective, we cannot say conclusively whether this skill precipitated complex tool use, language and symbolic rituals; whether an increasing dependence on these skills placed unique pressures on the ability to vicariously learn novel arbitrary sequences; or even whether these suites of skills co-evolved. Regardless, the interdependence between the ability to vicariously learn sequences and these uniquely human behaviours is unmistakable" (p7).

5.2.3. Cultural Evolution

"Cultural evolutionary theory" describes cultural change with the language of genetic evolution. Culture is presented as a "second inheritance system", which is "adaptive for coping with environmental fluctuations faster than those that can be tracked by genetic selection, but slower than those generally tracked by individual learning" (Nettle 2020 p2).

Nettle (2020) questioned this idea: "Culture is only a system of inheritance metaphorically, or as an idealisation, and the idealisation may lead us to overlook causally important features of how cultural influence works" (p1).

In genetic evolution, DNA replication occurs indifferently to the content of the message, for instance, while humans replicate culture "usually in the course of achieving a wide range of other purposes, other purposes that usually prescribe or favour transformation" (Nettle 2020 p4).

5.3. SOCIAL LIFE

A commonly held view of "biological evolution says that nature selects for selfishness. Always. Selfish genes increase survival, so are the ones that get passed on. If altruistic genes happen to poke their heads up, they are quickly whacked. In this reading, the desire to do good by others must be taught - usually with the threat of punishment by a wrathful God, censorious parent or nosy cop. The only underlying motive for any altruism is fear" (Churchland 2019 p45).

But this is not the case as social life, co-operation, and altruism is seen in many species of mammals and birds, and is a hallmark of much of human behaviour.

Churchland (2019) argued that the evolution of endothermy (ie: being warm-blooded) around 200 MYA is important. Being an endotherm requires lots of calories, and there is an advantage to being more intelligent to gain these calories (ie: the evolution of the cortex and a larger brain). However, a larger brain at birth makes the newborn vulnerable, and this led to the evolution of maternal (parental) care. Simplified, the biological solution seems to have been to modify the emotions associated with self-survival (fear when threatened, discomfort when hungry) so they are also aroused for baby-threat and baby-discomfort. In effect, the mammalian mother feels her babies are part of her, which indeed they are until birth. Sharing the attachment wiring, the baby becomes increasingly connected to its mother and father, further enhancing its chance of survival. In effect, evolution expanded the ambit of 'me' to include 'me-and-mine'" (Churchland 2019 p46).

The "me-and-mine" feeling widens to include others in our social group, and this, in time, goes with living in small, harmonious groups where survival was much better than alone. So, there is a "social instinct" which includes the urge to belong, as well as the evolution of emotions like empathy (Churchland 2019).

On the other hand, some would argue that 200 years of capitalism has encouraged individual selfishness. In consequence, this "capitalist personality" means that we are unable to deal with climate change (Schumaker 2018).

If not selfishness, then indifference (or "adiaphora"; Bauman and Donskis 2013). This describes "the consensus of indifference that enables consumer capitalism to fulfil its operative promise of ever-growing 'creative destruction'. As a result,... [Bauman and Donskis write] 'we are at risk of losing our sensitivity to the plight of others', something which applies equally to our socially sanctioned indifference toward future generations and the well-being of the planet" (Schumaker 2018 p50).

5.3.1. Empathy

Helping injured, distress or weak members of a species is relatively rare in non-human animals, though it is common among humans, and "appears to have an ancient evolutionary origin in Homo" (Sato et al 2019 p807). The underlying mechanism for helping behaviours seems to be empathy for others in distress.

Such empathy appears to be based on the sufferer's behaviour (eg: screaming; distressed facial expressions), or contextual cues (eg: injury; inability to escape from a trap) (Sato et al 2019).

Chimpanzees have been observed in the wild to respond with "empathy" - eg: lick a groupmate's injuries; wait for an injured individual when travelling; remove a snare from a trapped groupmate (Sato et al 2019). "These observations are informative because they suggest that chimpanzees respond to others' distress not only when seeing a behavioural cue (based on a specific emotion possibly developed for species-typical communication) but also when seeing a contextual cue (based on understanding a cause of distress); both observations together provide more stringent evidence for empathy in chimpanzees" (Sato et al 2019 p808).

But what about the emotional response in these situations? For example, humans report negative emotions ("empathetic pain") and show physiological responses when observing others in painful situations in experiments (eg: Goubert et al 2005).

There are limited experiments of this type with chimpanzees. Parr (2001), for example, measured skin temperature (as an indicator of physiological arousal) when chimpanzees watched a video of another chimpanzee being injected with a hypodermic needle. This produced a decrease in skin temperature, but so did the control video of a hypodermic needle by itself. "Thus, it remains unclear whether chimpanzees empathised with conspecifics in distress, or simply responded to the hypodermic needle as an aversive stimulus" (Sato et al 2019 p808).

Sato et al (2019) developed on this work in three experiments.

Study 1

This study investigated the observation in the wild that "chimpanzees tend to spontaneously approach others' injuries, rather than being afraid of or avoiding them. This is an important characteristic of these responses, because it may differentiate an other-regarding affective response or sympathetic concern from a personal fear or disgust" (Sato et al 2019 p809).

The participants were six chimpanzees at a wildlife sanctuary in Japan. Individually, they were presented with two images of chimpanzees on a video screen, and the direction of gaze was tracked. In the test condition, one image showed a chimpanzee with a bleeding injury and the other image no injury. The control condition used the same images but hid the injury. The order of presentation of the eight image pairs in each condition was counterbalanced, and the images were presented for six seconds. This study used the "preferential looking paradigm", which is commonly used with human babies.

The amount of time looking at one image was measured. The chimpanzees spent more time looking at the injured image in the test condition than the control condition, and this was significantly above chance. This finding established that chimpanzees pay more attention to injured than non-injured conspecifics.

Study 2

This study investigated whether chimpanzees would be physiologically aroused when viewing the injuries of others using thermal imagery to show changes in nasal skin temperature. Arousal is indicated by reduced temperature.

The same chimpanzees as previously were tested. The stimuli were a familiar human who appeared to cut their hand when slicing a banana without showing any behavioural reaction (test condition) (table 5.1) or just slice the banana (control condition). The thermal imaging was taken throughout the event, and for two minutes after.

- "In the test condition, the participant was exposed to an experimenter with a prosthetic wound and artificial blood on his right palm. The prosthetic wound was created from skin-coloured wax painted with reddish eye-shadow and artificial blood. In addition, a tube was hidden under the right sleeve, through which fake blood was pumped over the wound. At the beginning of the demonstration, the experimenter picked up a banana and attempted to cut it with a knife (with the prosthetic wound hidden in his hand). He slipped with the knife, appearing to cut his right palm, put the banana and knife down, showed the wound to the participant chimpanzee, and let the fake blood run by quickly removing the stopper from the tube" (Sato et al 2019 p813).

Table 5.1 - Details of the scenario in Study 2.

"Chimpanzees exhibited a greater decrease in nasal temperature in the test compared with the control condition" (Sato et al 2019 p815). This suggested that the chimpanzees were aroused by seeing the familiar human injuring themselves.

But the "chimpanzees exhibited decreased nasal temperature in both the test and control conditions, although the response was stronger in the test condition. This result may suggest that the stimulus presented in both conditions was arousing for chimpanzees to some extent. Importantly, we suspect that procedural factors may have also been involved. For example, it is possible that giving a sip of juice during the demonstration (to encourage chimpanzees to remain in front of the thermo-camera) caused a decrease in nasal temperature. It has been previously reported that gastro-intestinal activity can cause a drop in nasal temperature due to activation of the sympathetic nervous system at the initial stages of ingestion" (Sato et al 2019 p816).

Study 3

In this study, the explicit cue of blood was removed. In the test condition, the human stabbed themselves accidentally with a needle when picking up a piece of wood, while in the control condition the human stabbed the piece of wood. The chimpanzees showed no changes in nasal temperature in either condition. "This result may indicate that chimpanzees had difficulty in understanding others' pain without seeing familiar cues, such as a wound and blood. An alternative but related possibility is that direct experience is important to elicit empathic responses..." (Sato et al 2019 p818).

The researchers continued: "It is also possible that chimpanzees exhibited subtle responses that could not be captured by the thermal imaging technique. This speculation is based on the observation that a female adult (Mizuki) exhibited reduced nasal temperature at the very moment the needle penetrated the finger (and recovered immediately after). Note that we did not expect such a brief change, and thus our model did not fit the observed decrease. To capture such a subtle and short change, a measure of skin conductance may be more appropriate" (Sato et al 2019 p818).

Overall, Sato et al (2019) argued that these studies had made two key contributions:

a) Theoretical - "The current findings revealed that chimpanzees exhibited physiological arousal when seeing others' injuries. This finding corroborates the idea that chimpanzees can empathise with distressed others, even without behavioural cues such as emotional expressions, which may motivate chimpanzees to inspect injured groupmates" (Sato et al 2019 p820).

b) Methodological - The use of thermal imaging technology to measure physiological arousal, and "a real-life theatrical demonstration of an accident" (Sato et al 2019 p820).

To sum up, the chimpanzees showed a physiological response to others' injuries without behaviour reactions like screaming, but they do need explicit or familiar cues like blood.

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6. MISCELLANEOUS HUMANS

- 6.1. Agricultural societies
- 6.2. Human olfactory communication
- 6.3. Human impact on nature
    - 6.3.1. Ecosystems and climate change
    - 6.3.2. Urbanisation
    - 6.3.3. Conservation
- 6.4. Appendix 6A - Fish and pain
- 6.5. References

6.1. AGRICULTURAL SOCIETIES

The "development of agriculture is viewed as one of the most notable behavioural innovations in human history, because it is linked to population expansion, village settlement (sedentism), increased territoriality, and pronounced symbolic cultural practices, referred to as the 'Neolithic'" (Shaw et al 2020 p1).

Around 4000 BC/6000 YA, the move from the mobile Mesolithic lifestyle of fishing, hunting and foraging for wild foods occurred (Sheridan 2020).

DNA from ancient burial tombs of the Neolithic groups, as in Newgrange, Ireland, has found evidence of incest among elites (ie: an offspring of first-degree genetically related parents - siblings or parent/child) (Cassidy et al 2020). "This finding led the team to speculate that the elite... practised incest as a way of maintaining a dynastic bloodline. Such a strategy, which breaks a near-universal social taboo against incest, was also practised much later by ruling elites in ancient Egypt, in the Inca empire and in ancient Hawaii" (Sheridan 2020 p348).

6.2. HUMAN OLFACTORY COMMUNICATION

Human communication based on language (acoustic), facial expressions and gestures (visual), and touch (tactile) is uncontroversial, but "the suggestion that humans also use body-based olfactory information for communicative purposes has historically been often met by scepticism, ambivalence or even antipathy" (Roberts et al 2020 p1).

Historically, olfaction was viewed as less important in humans compared to "supersmeller" species (eg: mice; dogs) for various reasons including the small size of the olfactory bulb area of the brain relative to overall brain size. But "although supersmelling species respond more sensitively to certain odours, humans can match or even outperform them in detection of other odours. Humans can also undertake very sensitive olfactory tasks such as tracking an odour through a field or detecting the smell of a single Drosophila fly in a glass of wine" (Roberts et al 2020 p2).

Roberts et al (2020) explained the dismissal of the importance of olfaction to human as due to 19th century physiologists, and WEIRD and ODD biases today:

a) Physiologists - Paul Broca, for example, in the 1870s studying the brains of mammals classified them as "osmatic" (using smell) or "anosmatic" (not using smell) based on "the development of their olfactory bulb, hippocampus and the 'great limbic lobe' relative to the rest of the brain" (Roberts et al 2020 p1). Humans and other primates were anosmatic for him.

b) Western, educated, industrialised, rich and democratic (WEIRD) societies (Heinrich et al 2010) - Much of psychology is based on research with North American (or European) undergraduates. The upshot is that the view of poor human olfactory perception is because it is not seen as important in such societies. But this is not the case in the rest of the world.

c) Allied to the WEIRD bias is that "both researchers and participants tend to be relatively old (ie: prevalently adult), and they tend to live in societies that have become deodorised and desensitised to odours (ODD)" (Roberts et al 2020 p3) - This ignores the importance of olfaction in childhood, while the masking of body smells with deodorants, for instance, and other behaviours has desensitised the "Western nose".

Subsequently, Roberts et al (2020) outlined five main areas of current interest and research on human chemical communication:

i) Odour production - eg: genes and characteristic armpit odour.

ii) Odour reception - eg: sensitivity thresholds.

Eg: Oleszkiewicz et al (2020) reported work with a German sample who had impaired smell, and these individuals, for instance, "formed fewer odour associations with feelings and memories" (Roberts et al 2020 p7).

Eg: Self-sniffing of hands (Perl et al 2020) - "Although we are aware that we do this, such behaviour may covertly or sub-consciously provide continual updates on our emotional and physiological state, and be used to compare with the odours of people we interact with" (Roberts et al 2020 p7).

iii) Communication between mothers and children - "The relationship with the mother's odour starts even before birth, as babies learn the smell of the amniotic fluid and of foods she ingests, and becomes especially critical in the hours following birth, facilitating the process of finding and latching to the breast and accessing colostrum" (Roberts et al 2020 p7).

From the other side, mothers can detect their child's odour correctly better than chance, and rated it as more pleasant (Schafer et al 2020).

iv) Communication between potential partners - eg: detection of major histocompatibility complex (MHC) (related to the immune system) in body odours and mate choice.

v) Communication of emotional state and disease - eg: odours related to fear or aggression.

Fialova et al (2020) collected odours of winning and losing fighters in mixed martial arts contests. Animal studies have found that dominant individuals (ie: winners) have a more preferable odour to others, and this was expected by the researchers here. Roberts et al (2020) explained: "In the fighters, odours were judged to be more masculine, but less pleasant, attractive and intense, after the contest, regardless of the outcome. However, the results suggested that losing may lead to a particular reduction in ratings of odour pleasantness, as predicted, and is a further demonstration that human raters are capable of discriminating socially relevant cues from odour" (p8).

6.3. HUMAN IMPACT on NATURE

6.3.1. Ecosystems and climate change

Schmidt et al (2019) began: "Around the world, temperatures are increasing. To predict the consequences for local ecosystems, we typically rely on the assumption that we can predict future conditions from current trends, and that with climate change, species and communities will follow their climatic envelopes in an orderly manner" (p1).

How climate change actually manifests in specific areas could be different. Schmidt et al (2019) referred to a well-studied area of the Arctic: "Beyond the general trend of warmer and earlier summers and a retreating snow cover, large parts of the Arctic, and in particular, the High Arctic, were covered by unusually large amounts of snow in 2018. This pattern was particularly evident in Northeast Greenland and at the research station of Zackenberg, where the local snow precipitation deviated from long-term mean conditions by several standard deviations. At Zackenberg, this resulted in snow melt being extraordinarily delayed" (p2).

The late start of the snow-free season in 2018 had an impact on the ecosystem with plants unable to flower, and less resources for animals consequently. Young were born later and so had less chance of surviving. For example, the Arctic-breeding shorebird, sanderling (Calidris alba) rely on arthropod prey, and the mean body mass of adults in 2018 was significantly lower than for 2007-17 (44 g vs 58 g). This led to no breeding that year (Schmidt et al 2019).

Schmidt et al (2019) explained their concerns: "Arctic plants and animals are well adapted to life under extreme climatic conditions, and their longevity and temporally dispersed reproductive bouts enable them to cope with the large variability in environmental conditions, both within seasons and between years. Therefore, one non-breeding year like the one observed in 2018 is hardly devastating for High Arctic species. The worrying perspective here is that the 2018 conditions may offer a peep into the future: Climate change has already resulted in a variety of species and ecosystem-level responses of arctic organisms. With less sea ice in the Arctic, we can expect more and more variable amounts of snow in the future. It is now well established that climate change includes increased variance in climatic conditions. As a consequence, more extreme events like the 2018 situation in Northeast Greenland may soon be occurring more often than before" (pp3, 5).

6.3.2. Urbanisation

Urban humans produce waste, including food, both intentionally and unintentionally that many species can exploit. Anthropogenic food resources include litter, compost piles, and trash, but, in some cases, these may be nutritionally deficient (especially for young animals). Thus, "cities might act as ecological traps, in which the abundant yet (potentially) low-quality food resources attract animals but are unable to sustain a population... In other cases, however, anthropogenic subsidies may improve the condition of wild animals..., increase reproductive output..., and buffer adults in harsh winter months" (Townsend et al 2019 p2).

Human urban food waste is often meat-based fast food, with dietary consequences for human health, and non-human scavengers. For example, increased cholesterol levels have been found in urban populations of foxes, sparrows, rock iguanas, and green turtles (Townsend et al 2019).

An adequate supply of cholesterol is "critical to physiological function, playing essential roles in cellular membrane permeability, bile production, synthesis of steroid hormones (eg: cortisol, progesterone, testosterone), and calcium metabolism" (Townsend et al 2019 p2) [22]. While excessive cholesterol is linked to heart problems.

Townsend et al (2019) investigated cholesterol levels in two populations of American Crows (Corvus brachyrhynchos). An urban population was around the University of California at Davis (studied from 2012 to 2015), while the other was a more rural population in Clinton, New York (studied between 2016 and 2018). Measures of cholesterol (in blood) were taken from 140 nestlings in sixty-six nests in California and 86 nestlings in twenty-nine nests in New York.

There was also an experimental part to the study, where MacDonald's food was left close to ten family groups for up to six weeks.

The observational data showed that the plasma cholesterol of the nestlings increased with the urbanicity of the nest (as measured by nearness to roads) in the California population. The mean cholesterol level was significantly higher in the California than New York population.

The experimental data showed that the nests fed with fast food had nestling cholesterol levels higher than comparable unfed nests.

Urbanisation was negative associated with long-term survival of nestlings. But this was probably due to more than just the cholesterol level. "A complex array of factors is likely to play a role in these survival differences between urban and rural crows. Predator and disease pressures, for example, can vary with urbanisation, although the direction of these differences can vary geographically as well as with the predator or pathogen in question... Urbanisation is also likely to reduce hunting pressure and have variable effects on the frequency of other anthropogenic sources of mortality (eg: car collisions, entanglement in plastic, electrocution...). Diet could also play a role if urban food sources are deficient in key micronutrients, which

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[22] Schoech and Bowman (2003) found that increased cholesterol lead to earlier breeding, and increased reproductive success/output among Florida Scrub-Jays, for instance.

may be particularly important in early development" (Townsend et al 2019 p8).

In summary, Townsend et al (2019) stated: "We found no evidence that elevated cholesterol levels were costly for crows in our populations; indeed, elevated cholesterol was associated with better body condition in the New York (although not the California) population. We note, however, that we only monitored nestlings for 2-3 year after hatching. Elevated cholesterol might have costs that we did not detect, as the negative effects of excessive cholesterol levels can take years to manifest" (p8).

6.3.3. Conservation

Sekar and Shiller (2020a) challenged what they saw as conservationists' priority to protect species and populations rather than the welfare of individual animals - ie: "with limited exceptions, the most prominent international conservation organisations do not attempt to promote animal welfare in their mission or vision statements or to safeguard animal welfare in their readily available public policies. This contrasts with often robust ethics policies on a range of other social and environmental issues" (p629).

According to these authors, the concern for individual animals should occur because "animals think and feel" (Sekar and Shiller 2020a p630).

Arlinghaus et al (2020) found a "feelings-based approach" problematic "because there is substantial scientific uncertainty about whether taxa such as fish are sentient and, therefore, able to feel pain and suffer" (p180) (appendix 6A). They continued: "A pragmatic approach to animal welfare that relies on objective and measurable endpoints of animal well-being is more likely to gain support among stakeholders and be implemented in practice than a feelings-based framework that is based on concepts that are difficult to define and cannot be readily measured in many taxa" (Arlinghaus et al 2020 p180).

Lynch and Blumstein (2020) responded to Sekar and Shiller (2020a) that "more humane conservation tactics are often costlier. The money and resources spent on humane conservation practices detract from the resources available for other conservation projects" (p179). For example, aerial culling of feral horses in Australia costs less than 100 Australian dollars per horse compared to passive trapping at over 1000 dollars per horse (Lynch and Blumstein 2020). Contraceptives to control populations would be better, argued Sekar and Shiller (2020b).

Hampton et al (2020) argued that concentrating on the individual (what they called "compassionate conservation") "may, perhaps counter-intuitively, worsen animal welfare outcomes and make biodiversity conservation more difficult" (p180). Sekar and Shiller (2020b) countered: "The small minority of conservation organisations that do explicitly recognise animal welfare concerns have demonstrated that policies promoting animal welfare in conservation are practicable" (p181).

The threat of biodiversity loss, in 2010, led governments to set twenty targets (via the United Nations Convention on Biodiversity). But it has been suggested that one headline target would be better (Editorial 2020). For example, Rounsevell et al (2020) proposed keeping extinctions to less than twenty known species per year.

Others reject this idea because "biodiversity is multi-faceted" (Editorial 2020). Furthermore, twenty extinctions per year would be difficult when around one million species are believed to be on the brink of disappearing. So, "how to choose which species to conserve, and who should make such choices. Would a single number give equal weight to all threatened species, or should some species that are important to livelihoods and to ecosystem function be given priority for protection" (Editorial 2020 p7)?

Lasting damage to the planet could also occur without any species going extinct (Editorial 2020).

6.4. APPENDIX 6A - FISH AND PAIN

Key (2016) began a debate on fish and the experience of pain [23] by arguing that they lacked the appropriate physiology (eg: neocortex) and so did not feel things.

On the other side, experimental work (Sneddon 2003) has shown that fish produce physiological and behavioural responses to pain and to analgesics similar to mammals (eg: trout injected with bee venom breathed faster and rubbed the injected site on the gravel on the tank floor) (Safina 2018).

"Nerves, brain structure, brain chemistry and behaviour - all evidence indicates that, to varying degrees, fish can feel pain, fear and psychological stress" (Safina 2018 p11).

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[23] See https://animalstudiesrepository.org/animsent/vol1/iss3/1/.

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7. SPERM COMPETITION

7.1. Introduction
7.2. Social status
7.3. Fishes
7.4. Within-ejaculate competition
7.5. Appendix 7A - Sexual parasitism
7.6. References

7.1. INTRODUCTION

Simmons and Wedell (2020) described Parker's (1970) article fifty years ago on the evolutionary consequences of sperm competition as "nothing short of a scientific revolution" (p1).

To call it a "scientific revolution" means a new paradigm (Kuhn 1970). "For a new paradigm to become established, Kuhn [1970] argued that it must preserve a large part of the accumulated knowledge that has already accrued, it must resolve some generally recognised problem that can be met in no other way, and it must have significant promise for future problem-solving" (Simmons and Wedell 2020 p1).

Parker (1970) developed Darwin's (1871) idea of sexual selection by emphasising that this continued after mating, particularly where females mated with multiple males.

Parker (1970) had written about insects, his area of interest, and, maybe not surprisingly, sperm competition gained little interest until the 1990s, and only after articles and books had developed it (eg: Thornhill and Alcock 1983) (Simmons and Wedell 2020).

Sperm competition is the product of females mating with multiple males (polyandry). It is also known as "post-mating pre-zygotic" (PMPZ) interactions (ie: after mating but before fertilisation) (Garlovsky et al 2020).

Sperm competition can be seen in the evolution of reproductive traits like gamete cell surface proteins, male seminal fluid proteins, female reproductive tract (eg: length), and sperm shapes/sizes/speed (Garlovsky et al 2020).

7.2. SOCIAL STATUS

According to sperm competition theory, "males should allocate available resources to ejaculates prudently, according to likely success in sperm competition" (Bayram et al 2020 p1). But what does this mean in practice because ejaculates are made up of "a complex mixture of sperm and seminal fluid proteins" (Bayram et al 2020 p1)?

Research has found that seminal fluid content can vary with sperm competition, and with male social status. In species with hierarchical social systems, the dominant male has greater access to females both in terms of frequency of mating and optimal time to mate relative to ovulation. "In this scenario, theoretical models predict that a subordinate male, mating in a disfavoured role, should increase investment in sperm production to compensate for an inherent disadvantage during sperm competition. Additionally, it is predicted that males mating in a disfavoured role should increase the allocation of resources to other, non-sperm, components of the ejaculate" (Bayram et al 2020 pp1-2). The non-sperm components (ie: seminal fluid proteins) may act as a "copulatory plug", which blocks rival male sperm while promoting movement of the owner's sperm (as in rodents) (Bayram et al 2020).

Subordinate males would benefit from more production of these proteins involved in the "copulatory plug". Bayram et al (2020) explored this idea in the house mouse (Mus musculus domesticus).

Males who are dominant defend territories, are preferred by females, and sire more litters, but females also mate with more than one male which gives opportunities for subordinate males.

In a laboratory colony, the researchers assessed the dominance hierarchy based on urinary scent marking (which dominant males do more of), and thus distinguished dominant and subordinate males (along with controls who were kept separately). Comparing the three groups, Bayram et al (2020) explained: "Dominant males invested more in ejaculates overall, with significantly higher sperm counts and larger seminal vesicles than subordinate and control males. However, subordinate males produced a more concentrated protein secretion from their seminal vesicles, and we found subtle but consistent differences in the seminal fluid protein composition of male mice according to their social status" (pp6-7).

These findings partly support the sperm competition theory predictions:

i) Not supported - Dominant males produced more sperm. This may be because "some aspects of subordinate males' reproductive function is being suppressed in the presence of a dominant male" (Bayram et al 2020 p7).

ii) Supported - Subordinate males produced more seminal fluid proteins in the ejaculate which could act as the "copulatory plug".

Bayram et al (2020) ended by emphasising that sperm competition theory should consider the evolution of the entire ejaculate and not just the sperm content.

7.3. FISHES

Fish exhibit both internal and external fertilisation among the many different species, and even within the same species (Fitzpatrick 2020). With external fertilisation, the sperm and eggs are released simultaneously into the water. "External fertilisers are assumed to have less control over paternity, as external release of gametes allows for group spawning and sneaking behaviours. Sperm competition levels are, therefore, generally thought to be higher in externally fertilising species compared with internal fertilisers" (Fitzpatrick 2020 p2).

Fitzpatrick (2020) surveyed the evidence for this assumption using data on forty-one external fertilising species and 49 internal fertilisers, as well as eight species with male pregnancy (eg: seahorses) (appendix 7A).

The key predictions were:

a) Sperm number: relative testes size - Males will have a larger testes size relative to body size with greater sperm competition, irrelevant of the fertilisation mode.

b) Sperm number: sperm allocation - More sperm will be produced with increased sperm competition, but external fertilisers "may be better able to assess the number of competitors present when allocating sperm, particularly compared with sequentially mating internal fertilisers" (Fitzpatrick 2020 p2).

c) Sperm quality - "Slower but longer-lived sperm are predicted with increasing sperm competition in internal fertilisers. Longer and faster-swimming sperm (that are short lived) are expected to be favoured in external fertilisers where sperm must rapidly reach and fertilize eggs before those of rivals..." (Fitzpatrick 2020 p2).

Fitzpatrick (2020) drew the following conclusions from his analysis:

i) Sperm competition is higher in internally than externally fertilising species based on the proxy measure of females mating with multiple males. "This unexpected finding may either arise from sampling bias or demonstrate the importance of prolonged female sperm storage in internal fertilisers as a moderator of sperm competition levels in fishes" (Fitzpatrick 2020 p7).

ii) Overall, increased sperm competition is associated with increased sperm number. But there are exceptions. For example, males who guard females produce less sperm unaware that there are competing "sneaker males".

iii) Sperm swimming speed predicts fertilisation success in both modes of fertilising.

iv) "The importance of seminal fluid as a mediator of ejaculatory responses to variation in sperm competition is beginning to come into focus in fishes. Whether the role of seminal fluid differs based on fertilisation mode remains an open question" (Fitzpatrick 2020 p7).

v) "Interactions between ovarian fluid and sperm have the potential to alter selection on ejaculates and impact patterns of sperm evolution in both external and internal fertilisers" (Fitzpatrick 2020 p7).

vi) The findings are based on the well-studied species of fish, and, Fitzpatrick (2020) ended, "[E]xpanding our gaze to the murkier waters of the fish tree of life will help advance our understanding of sperm competition in fishes and the importance of fertilisation mode in shaping evolutionary responses in ejaculates across animals" (p7).

7.4. WITHIN-EJACULATE COMPETITION

Sperm competition theory focuses on the competition between the ejaculates of different males, but Sutter and Immler (2020) added a different slant, saying that "because in the vast majority of species, sperm from one male generally outnumber available eggs, the competition among sibling sperm produced by one male is potentially intense" (p1). They called this "within-ejaculate competition" (as opposed to "between-ejaculate competition").

Individual sperm in an ejaculate share about 50% of the genes of all the sperm. This means that there are different traits (phenotypic variation) between sperm, and this opens the possibility of selection pressure on sperm traits. This is the first of three criteria for evolution here outlined by Sutter and Immler (2020). The other two are that "sperm phenotypes must be heritable; and... sperm phenotypes need to affect fitness" (Sutter and Immler 2020 p2).

There is limited evidence for these ideas in animals [24], partly because of "lack of technologies" to test them (Sutter and Immler 2020).

Sutter and Immler (2020) ended with a series of questions for researchers:

i) The issue "around identifying the 'best' sperm in an ejaculate: is there a 'best' sperm and if so, which one is it? Which traits contribute to the success of a sperm in within-ejaculate sperm competition? Do these depend on environmental conditions?" (Sutter and Immler 2020 p5).

ii) This is "whether variation - both genetic and phenotypic - among sibling sperm is systematic as opposed to arising from simple 'production errors'" (Sutter and Immler 2020 p5).

iii) What is the best way to study within ejaculate sperm competition?

7.5. APPENDIX 7A - SEXUAL PARASITISM

Deep-sea anglerfishes (Ceratioidei) show "a distinctive mode of reproduction" called "sexual parasitism" (Swann et al 2020). The male is tiny, and he attaches (either temporarily or permanently) to a gigantic female. "In some taxa, attachment is followed by fusion of epidermal and dermal tissues and, eventually, by connection of the circulatory systems so that the male becomes permanently dependent on the female for nutrients, with the pair becoming a kind of self-fertilising chimera" (Swann et al 2020 p1608). Females can have more than one male attached at the same time.

The fusion should produce an immune response in both parties. Swann et al (2020) studied thirty-one specimens from ten species of Ceratioidei, and found changes to the immune system that have evolved to allow sexual parasitism. For example, temporarily-attached males lack certain genes related to the production of anti-bodies. In permanently-attaching species, three changes in immune-related genes were found.

Swann et al (2020) raised this point of caution: "Whether the evolutionary advantage of sexual parasitism is itself sufficient to drive changes in the immune system or whether other evolutionary forces first lead to changes in the immune system, which are then exploited

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[24] "The most convincing evidence for within-ejaculate competition comes from studies in a range of plants" (Sutter and Immler 2020 p3).

for the evolution of sexual parasitism, is an important question to resolve in future studies" (p1613). These researchers favoured the latter because some other species of fish (non-sexual parasites) have similar immune system changes.

But how have the anglerfishes survived the immune system changes? One answer is the "reorganisation of innate immune defences to provide efficient protection against pathogens" (Swann et al 2020 p614).

Swann et al (2020) also made this point: "Although we consider it unlikely, we cannot exclude the possibility that anglerfishes have evolved an entirely new type of adaptive immune system" (p614).

Finally, Swann et al (2020) concluded that studies like this "hold promise to learn about potential strategies to enhance innate immune defences in immune-deficient patients" (p614).

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8. SLEEP AND CYCLES

- 8.1. Activity and sleep among primates
    - 8.1.1. Sleep duration and intensity
    - 8.1.2. Sleep homeostasis
    - 8.1.3. Sleep sites
    - 8.1.4. Comparative sleep
- 8.2. Birds and sleep
- 8.3. Lunar cycle
- 8.4. Cockroaches and body clock
- 8.5. Night vision
- 8.6. Body temperature
- 8.7. Adolescent sleep and mental health
- 8.8. Menstrual cycle research
- 8.9. Appendix 8A - Nests and weather
- 8.10. References

8.1. ACTIVITY AND SLEEP AMONG PRIMATES

Animals tend to be categorised as diurnal (ie: active during the day), nocturnal (ie: active at night), or crepuscular (ie: active at dusk and dawn). Tagg et al (2020) noted that this simple categorisation process may lead to "observational bias, which is likely to lead to biases in the assumptions we make about animals and their behaviour patterns. For example, all anthropoids, except owl monkeys..., are categorised as diurnal and are, therefore, generally not studied during night hours as they are ubiquitously assumed to be inactive throughout the night. However, numerous accounts suggest that wild diurnal monkey species exhibit various types of activity during night-time hours, including travelling by gelada baboons..., olive baboons..., and vervet monkeys...; playing, eating, and mating by rhesus macaques...; feeding by Guizhou snub-nosed monkeys...; vocalising by Barbary macaques...; and moving sleeping sites by Japanese macaques" (pp510-511).

Nocturnal activity by diurnal species can be studied with new technologies like GPS collars, and camera traps, as human observation is difficult.

Tagg et al (2020) used camera traps in their study of of chimpanzees' night-time behaviours. Data from camera traps at 22 sites in Africa uploaded at public websites prior to February 2017 were analysed. Volunteers ("citizen scientists") were recruited to record the presence of a chimpanzee in camera trap footage, and to categorise the behaviour as "movement" (eg: walking, running), "on location" (eg: climbing a tree), "social" (eg: grooming), and "feeding". The time of the nocturnal activity was also noted.

In total, there were 119 independent observations at night. Nocturnal activity was a very small proportion of all chimpanzee activity in a 24-hour period (ie: 2%), and males were the most observed in terrestrial nocturnal activity (most commonly "movement") [25]. Nocturnal activity was higher at sites with less human activity, high temperatures (appendix 8A), and forested areas, but illumination (eg: full moon) had no effect.

The use of camera traps could be evaluated thus. The advantages to this technology include its non-invasive nature, the ability to study animals not habituated to humans, and in areas and at times when human observers not present (Tagg et al 2020).

The camera traps in this study did not capture nocturnal activity, if any, in the trees. Also "it is likely that camera-trap capture rates are reduced in dark conditions, so it might be possible for chimpanzees to move about at night without triggering a camera; or that chimpanzees are sensitive to the light or sound emitted by cameras, which may be heightened at night when the contrast may be greater, and cameras may be avoided" (Tagg et al 2020 p522).

8.1.1. Sleep Duration and Intensity

Sleep duration, and intensity (ie: amount of time in slow wave sleep; SWS) are both important, and where duration is reduced, intensity increases. "Sleep intensity is relevant for understanding sleep in wild animals, where individuals are faced with many risks when sleeping, including increased predation, dangers from inclement weather, social competition, and opportunity costs of foraging, searching for mates, or caring for offspring" (Samson et al 2018 p579).

Because of such risks, Fruth et al (2018) asked, "Why has evolution not eradicated sleep?" (p499). One answer is because of the physiological functions of sleep, like energy saving and recuperation, and helping memory consolidation.

On the island of Madagascar there are a variety of lemur species, and they differ in their activity patterns - cathemeral (activity throughout the 24-hour period)

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[25] "Males have a larger body size compared to females which may afford them more security for night-time activity, as is argued for male gorillas nesting closer to the ground than females... It is possible that males may wake more at night due to the nature of the activities carried out at night: males, for example, may be more likely to engage in territory patrols and this can occur at night... However, many females and immature individuals were also observed exhibiting nocturnal activity, so it is not solely an adult male activity" (Tagg et al 2020 p523).

(eg: crowned lemur) or diurnal (eg: Coquerel's sifaka). Samson et al (2018) studied seven species of captive lemur (table 8.1) to understand sleep duration and intensity. Data were collected with actigraphic sensors on collars, and video-recording.

After baseline measures were made, sixteen lemurs were sleep deprived for one night, and the sleeping site (indoor or outdoor) was also varied. The diurnal species (Coquerel's sifaka) (figure 8.1) was most sensitive to disrupted sleep. All species' sleep was impacted by their sleeping site.

Samson et al (2018) explained: "Sleep is a time of great risk for animals, potentially resulting in selection of safe sleep sites and greater vigilance when a safe site is unavailable... We see signatures of this risk in our data, with lower sleep intensity when animals sleep outside, as compared to greater sleep intensity when sleeping indoors where it is safer. Lower sleep intensity in outdoor-sleeping lemurs may have been a result of abiotic (eg: inclement weather, variation in temperature, and lunar phase) and biotic stimuli (eg: calls from predatory animals)" (p586).

Common Name	Latin Name
Diurnal:	
Coquerel's sifaka	Propithecus coquereli
Full Cathemeral:	
Crowned lemur Blue-eyed black lemur Mongoose lemur	Eulemur coronatus Eulemar flavifron Eulemur mongoz
Moderate cathemeral:	
Ring-tailed lemur Red ruffed lemur Black and white ruffed lemur	Lemur catta Varecia rubra Varecia variegata

(Based on table 1 p580 Samson et al 2018)

Table 8.1 - Species of lemur in study by Samson et al (2018).

(Source: Ltshears; https://commons.wikimedia.org/wiki/User:Ltshears)

Figure 8.1 - Captive Coquerel's sifaka.

8.1.2. Sleep Homeostasis

The balance between the duration of sleep and waking is called "sleep homeostasis". Put simply, during the waking period there is a build up of "sleep pressure" which eventually causes the individual to sleep. This pressure appears to be linked to adenosine released in the basal forebrain area (Peng et al 2020).

Using optogenetics, which involved a green fluorescent protein, Peng et al (2020) were able to measure adenosine levels in laboratory mice over 24 hours. The fluorescent protein was designed to respond to the amount of adenosine in the basal forebrain. Optical fibres were inserted into the brain to measure the fluorescence.

Adenosine was found to be high during waking and low during NREM sleep. Interestingly, adenosine was also high during REM sleep.

When Peng et al (2020) destroyed the neurons that released adenosine, the mice spent more time awake than controls. These mice also spent less time in NREM sleep after sleep deprivation [26]. Normally, "sleep rebound" (ie: catching up sleep after deprivation) involves increased periods of NREM sleep.

8.1.3. Sleep Sites

Svensson et al (2018) focused on 36 species of lorisiforms (eg: red slender loris (Loris tardigradus); brown greater galago (Otolemur crassicaudatus)) using their data from fieldwork in various countries (12 in Africa and six in Asia), and published studies. Sleep sites were categorised into five groups:

- Nests (self-built or built by other species)
- Tree holes or hollows
- Dense tangles of vegetation
- Tree branches/forks
- Bamboo thickets.

The most popular site was tangles (used by 67% of species) [27], followed by holes and branches (both 44%). Individuals from the same species often used different sites (eg: 62% of species that used tangles also used branches) [28].

"Predation avoidance appears to be a main factor in sleep site choice" (Svensson et al 2018 p572). Note that most of these species of primate are nocturnal, and so would be sleeping during the day. "Most lorisiforms enter their sleep sites around sunrise and leave around sunset; several are active during twilight, or briefly, during daytime" (Svensson et al 2018 p564). No species was cathemeral, or showed multiple short sleeps in the 24-hour period.

The data supported a hypothesis by Kappeler (1998), which proposed that the "use of nests and tree holes is linked to having altricial infants that are not able to cling to fur, thus providing them with a relatively safe location while adults forage" (Svensson et al 2018 p572).

8.1.4. Comparative Sleep

Samson and Nunn (2015) analysed the evolution of

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[26] Sleep deprivation for six hours involved gentle handling of the mice in their home cages to stop them falling asleep.

[27] "Sleeping in tangles of dense vegetation reduces detection from predators, provides protection from the elements and facilitates rapid escape, especially for smaller lorisiforms..." (Svensson et al 2018 p573).

[28] "The use of different types of sleep sites within the same species of lorisiform suggests these species may be opportunistic generalists that are able to use the range of habitat features available to them or respond to varying sleep site selection pressures" (Svensson et al 2018 p573).

human sleep in comparison to other primates. They proposed that "human sleep has been shaped by risks and opportunity costs, with risks involving increased predator and conspecific threats from sleeping on the ground, and opportunity costs of sleep involving time lost for building and maintaining social bonds, and fewer opportunities for individual or social learning" (Nunn and Samson 2018 p602).

Nunn and Samson (2018) extended this work using published data on aspects of sleep in thirty non-human primate species. Comparing these species on characteristics like body mass, predation risk, brain size, and foraging needs, predictions can be made about humans.

For example, humans were predicted to evolve a total sleep time of 9.5 hours (compared to the actual average of seven hours), and to spend 14% of that in REM sleep (compared to over 20% in reality). What this means is that specific factors were involved in the evolution of human sleep.

One possibility is that humans are diurnal, whereas many primates are active at night (nocturnal). Nunn and Samson (2018) speculated that "nocturnal species may prefer to forage in maximal darkness to reduce predation risk; hence, they may benefit from becoming active only after full darkness has been reached. This would effectively give them more time for sleep" (p609). These researchers continued: "In addition, nocturnal species often live in smaller groups (or solitarily), and often have concealed sleep sites that may reduce predation during both day and night, thus relaxing predation risk at the sleep site and favouring more sleep" (Nunn and Samson 2018 p609).

Another factor noted by both studies was the terrestrial lifestyle of humans, including sleeping on the ground. "This lifestyle would have exposed early humans to greater predation risk, and potentially to greater threats from hostile conspecifics, who would have been able to locomote more effectively on the ground at night (as compared with primates moving arboreally at night in the trees)" (Nunn and Samson 2018 p609) [29].

In terms of opportunity costs, sleep reduces the time available for learning (both individually and socially), which is crucial to humans. Nunn and Samson (2018) rated this factor as the most important evolutionary pressure to reduce time sleep time. This is supported by the larger than expected amount of REM sleep, and this type of sleep is associated with memory consolidation.

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[29] A key step for hominins was the building of nests on the ground, which became more sophisticated (and permanent) shelters in time (Fruth et al 2018).

8.2. BIRDS AND SLEEP

Artificial light at night disrupts sleep in both humans and non-humans. Aulsebrook et al (2020) reported three recent experiments with birds and miniature data loggers to record brain activity.

Experiment 1 - Nine domestic pigeons (Columba livia) were tested over three consecutive nights - darkness (1st night - baseline), white light (equivalent to street lighting) (2nd night - treatment), and darkness (3rd night - recovery. "During the treatment night, all aspects of sleep architecture were disrupted and the percentage of sleep allocated to REM [rapid-eye movement] sleep was reduced, relative to baseline. The prolonged reduction in NREM [non-REM] sleep SWA [slow wave electrical brain activity] was partially, but not consistently, due to increased eye opening" (p3657) [30].

Some sleep was recovered in the day following the treatment night, and in the recovery night. Overall 3.3 hours of NREM sleep was lost, and only 1.4 hours of it recovered.

Experiment 2 - Eight pigeons were exposed to white or amber light for a night (using the same experimental design as previously). The colour of the light did not vary the findings that confirmed Experiment 1.

Experiment 3 - Eight Australian magpies (Cracticus tibicen tyrannica) here, and the light (white or amber) was switched on for part of the night only (4 of twelve hours). The sleep was more disrupted by the white than amber light, and more than the pigeons under white light. "On average, magpies lost 76% of NREM sleep under white light, whereas pigeons lost only 44% over the equivalent time period. Under amber light, the amount of NREM sleep was more similar between the two species: magpies lost 48% of NREM sleep relative to baseline, whereas pigeons lost 37%" (Aulsebrook et al 2020 p3659).

The research "cannot identify the mechanisms by which artificial light at night affects avian sleep" (p3660), but the researchers speculated that melatonin changes were involved in disrupting the regulation of sleep (Aulsebrook et al 2020).

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[30] Sleep architecture is "the quantitative structure and patterning of sleep and includes measures such as total sleep time (TST), durations of rapid eye movement (REM) and non-REM sleep..., the cycling of NREM and REM (cycle length), and the distribution of sleep (ie: monophasic, with one sleep bout, or polyphasic, with multiple sleep bouts) throughout the 24-hr period" (Nunn and Samson 2018 p602).

8.3. LUNAR CYCLE

The lunar cycle (30 days) has a powerful influence on many animals, including in foraging behaviour, predator-prey interactions, and reproduction. "Dark nights restrict foraging activity to periods of twilight around dusk and dawn, while moonlit nights appear to relax this temporal constraint" (Norevik et al 2019 p2).

This, in turn, can influence migration. The speed of migration will depend on daily food intake, as in the case of the "visual hunting nocturnal insectivore and long-distance migrant", the European nightjar (Caprimulgus europeaus).

Norevik et al (2019) recorded the movements of thirty-nine individuals migrating between north European breeding areas and over-wintering in southern Africa. The birds were fitted with GPS tags and data loggers using a full body harness in Sweden (for the migrations in 2015 to 2018).

Outside of the migration period, the nightjars were primarily crepuscular (ie: active around dusk and dawn), but they were also more active on moonlit than dark nights.

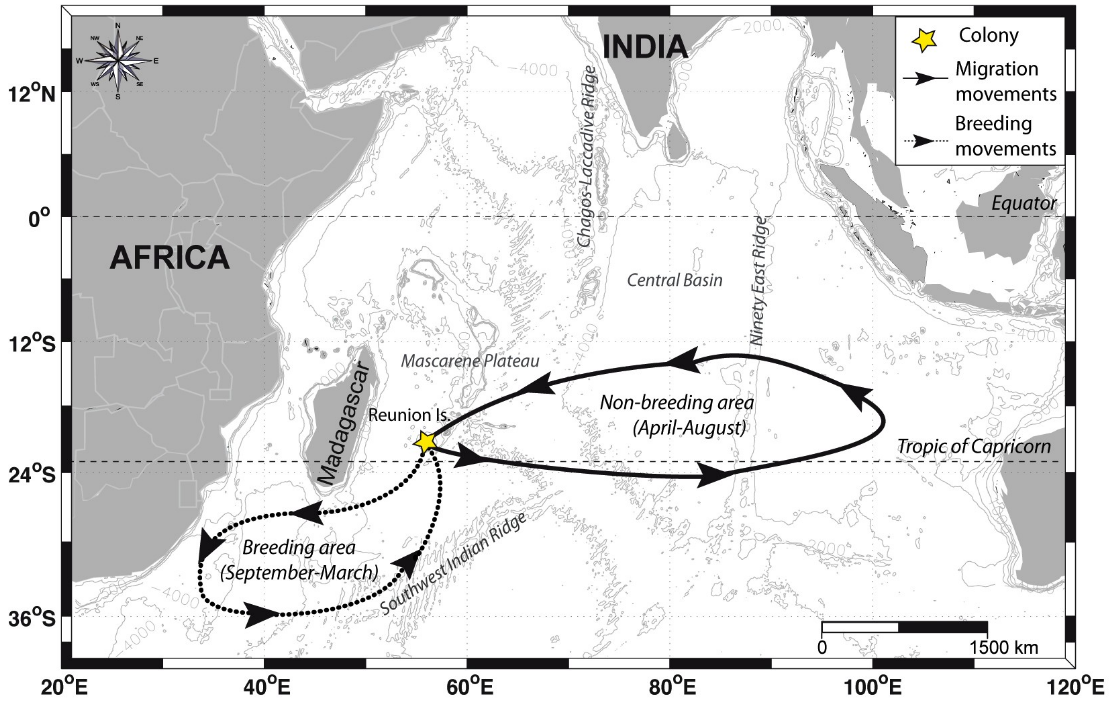
Migration is triggered by "preferred departure fuel load" (ie: sufficient body fat). It was predicted that more birds would depart "after periods of moonlit nights if moonlight promotes fuel accumulation" (Norevik et al 2019 p2). This was supported by the data which showed a peak in travel eleven days following full moon.

So, the lunar cycle in the form of moonlit nights (especially around full moon) influenced pre-migration fuelling and consequently migration departure. But there were other factors that influenced migration departure, like wind. "For example, a tail wind may trigger departure from a stopover before the optimal fuel load has been reached, which leads to sub-optimal arrival with respect to the lunar cycle at the next stopover" (Norevik et al 2019 pp4-5).

Cyclical behaviours like breeding and migration are triggered by a variety of cues, including temperature, rain, food supply or nest site availability (Pinet et al 2011). The lunar cycle is one those cues.

Pinet et al (2011) studied the Barau's petrel (Pterodroma baraui) with GPS and data loggers. The birds were based on Reunion Island in the Indian Ocean. Data were available for forty-one individuals between February 2008 and 2010.

The at-sea behaviour (ie: the proportion of time spent on the water) followed an annual cycle divided into two equal "seasons" (breeding and non-breeding) (figure 8.2). Time spent resting at sea was significantly less in



(Source: Pinet et al 2011 figure 1)

Figure 8.2 - Movements of Barau's petrels during their two "seasons".

the breeding season. Length of day (photoperiod) was influential here.

Night-time at-sea activity showed a cycle of 29.2 days. "Birds spent significantly less time resting on water during full moon where they spent up to 80% (maximum activity: 11.9 h per night) of their time in flight. Overall, birds responded more clearly to the lunar cycle during the non-breeding season... compared to the breeding season" (Pinet et al 2011 p4). It was hypothesised that higher levels of moonlight intensity aided visual foraging, and more prey was available around the full moon. "Moonlight is known, for example, to affect the process of vertical migration of nekton that could increase the number of prey in the sub-surface layer where seabirds forage. Barau's petrels could therefore opportunistically increase their at-sea activity to take advantage of this higher prey abundance" (Pinet et al 2011 p6).

Pinet et al (2011) concluded: "To our knowledge, this is the first study to document a mixed regulation of the behaviour of a wild bird by photoperiod and moon phases throughout its annual cycle" (p1).

The diel vertical migration (DVM) of zooplankton, squid and fish to the surface of the ocean at night can be lower on bright nights (Cruz et al 2013). So, it would be an advantage for bird predators to be more active in foraging during the darker parts of the lunar cycle. Cruz et al (2013) showed this with the swallow-tailed gull (Creagrus furcatus) (a pelagic (open sea) seabird) based on the Galapagos Islands, Ecuador.

Fifty individuals were fitted with activity loggers, but only 46 devices were recovered, and 37 provided full data for the study period in 2010.

The amount of time the birds spent wet (ie: hunting at-sea) was significantly higher during the darkest periods of each month, and peaked at the new moon. The birds capture their prey by surface plunging to a maximum of one metre depth, so they are dependent on the DVM, and consequently have adjusted "their daily patterns of foraging behaviour to match activity patterns of their prey" (Cruz et al 2013 p5).

Many animals strongly influenced by light live at the extremes of the planet where there are large seasonal changes in day length. Thus, researchers look for species living near the equator where day length varies little across the year as a control.

Fernandez-Duque et al (2010) reported an example with a population of Azara's owl monkeys (Aotus azarai) living in northern Argentina. Actimeter collars were fitted on ten individuals and data were available for up to eighteen months between 2003 and 2005.

"The activity of the owl monkeys was predominately restricted to dawn and dusk, and had a nocturnal component that was clearly associated with the lunar cycle" (Fernandez-Duque et al 2010 p2) [31]. Nocturnal activity was significantly higher during full-moon nights (52% of daily total activity) than new-moon ones (26%). During the study period, there were three lunar eclipses where the full moon was hidden, and the monkeys showed little activity on these nights (Fernandez-Duque et al 2010).

8.4. COCKROACHES AND BODY CLOCK

Radiofrequency (RF) fields produced by modern technology are "suspected to interfere with biological processes" (Bartos et al 2019 p1).

Bartos et al (2019) investigated RF and magnetic fields (MF), and the circadian clock of forty adult German cockroaches (Blatella germanica) over fourteen days. Three intensities of MF and three intensities of RF

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[31] "It is still a matter of controversy whether ancestral primates were nocturnal, diurnal or had patterns of activity that involved activity during both night and day" (Fernandez-Duque et al 2010 p4).

field (along with controls) were tested.

The movement of the insects was recorded per five-minute period to establish the baseline circadian rhythms. Weak MF and RF fields slowed down the cockroach's biological clock. The upshot was that the insects were more active.

The mechanism of impact may be a protein (called "Cry") which is involved with the biological clock (eg: fruit flies; Yoshii et al 2009).

8.5. NIGHT VISION

Some animals not only see at night, but can distinguish colours. For example, in an experiment (Kelber et al 2002), hawkmoths were able to learn to associate a blue or yellow artificial flower with a reward even in light levels as low as dim starlight (Dance 2019) [32].

One problem for vision is "noise" (eg: light sensitive molecules occasionally trigger randomly and spontaneously), which is not an issue in broad daylight when many photons are hitting the eyes. One solution in darkness is to "boost" the signal through combining individual photoreceptor images in the eye before being sent to the optic area of the brain (known as "spatial summation"). There is also "temporal summation" which slows the response of photoreceptor cells, and hence they are combined as they head to the optic area of the brain. Both methods improve perceived brightness at the expense of the sharpness of the image (Dance 2019).

8.6. BODY TEMPERATURE

The core body temperature of mammals is controlled at around 37 °C (known as endothermy), with the exception of hibernation or torpor, where the body temperature can drop by 5, 10 or more °C [33]. In the other direction, fever (increased body temperature) is used to slow the replication of infections (Saper and Marchado 2020).

Control of body temperature (thermoregulation) is done by neurons in the pre-optic area of the hypothalamus in the brain. It is believed that the warming of the skin, for instance, triggers neurons which release the neurotransmitter GABA, and other regions of the brain are caused to produce cooling (Saper and Marchado 2020).

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[32] Similar experiments have been done with carpenter bees, and geckos (Dance 2019).

[33] For example, laboratory mice have been observed to show a daily torpor (for less than 24 hours) where the metabolism slows down (hypometabolic state) (Takahashi et al 2020). If deprived of food they alternate between two survival strategies - high-risk food searching behaviour and energy-conserving torpor (eg: almost half reduction in metabolic rate) (Hrvatin et al 2020).

Two recent studies with rodents (Takahashi et al 2020 and Hrvatin et al 2020) have found specific genes and neurons involved in the pre-optic area related to torpor or hibernation.

8.7. ADOLESCENT SLEEP AND MENTAL HEALTH

"Healthy sleep" includes getting the right amount, at the appropriate times, and without sleep disturbances or problems (Orchard et al 2020).

Healthy sleep can be negatively impacted by behaviours, and by ageing-related changes. For example, during adolescence the circadian rhythms change to sleep later (eg: increased alertness around midnight) (Orchard et al 2020). Consequently, on school nights, adolescents have a shorter sleep duration, while there is "growing evidence that poor quality and insufficient sleep is linked to cognitive, emotional and behavioural dysregulation" (Orchard et al 2020 p1126).

Orchard et al (2020) investigated this, specifically with reference to mental health, using data from the Avon Longitudinal Study of Parents and Children (ALSPAC). This longitudinal study began in 1991-2 in south-west England (Avon county) with over 14 000 pregnant women.

The data of a sub-sample of 5033 offspring were analysed at ages 15, 17, 21 and 24 years old. Measures were taken of sleep patterns and quality, and of anxiety and depression. For analysis purposes, three groups were distinguished at age 15 - (i) no anxiety/depression, (ii) anxiety diagnosis, and (iii) depression diagnosis.

The participants in the depressed group had significantly less sleep at age 15 years old than the other two groups (cross-sectional analysis), and less total sleep and poor sleep quality at this age significantly predicted anxiety and depression later (longitudinal analysis). Total sleep time at weekends was not significant.

Research generally suggests that "late sleep onset and fixed waking times on school days create chronic sleep restriction during adolescence, and that adolescents with delayed sleep are particularly vulnerable" (Orchard et al 2020 pp1131-1132).

Table 8.2. summarises the main methodological issues of this study.

STRENGTHS	WEAKNESSES
1. Both cross-sectional and longitudinal data analysed.	1. The sample was mostly White British.
2. Large sample.	2. The measures were self-report.
3. Assessment of sleep, and anxiety and depression by standardised questionnaires.	3. Some aspects of sleep were not measured (eg: "wake after sleep onset") (Orchard et al 2020).

Table 8.2 - Key strengths and weaknesses of Orchard et al (2020).

8.8. MENSTRUAL CYCLE RESEARCH

Providing evolutionary explanations for behaviours that appear to vary across the menstrual cycle has become popular in the last fifteen years (varying between voting tendencies and tips earned by lap dancers) (Kiesner et al 2020). "However, a failure to consider the complexity and interdependent dynamics of the many biological, psychological, and social changes of the menstrual cycle significantly limits the conclusions that can be drawn from these studies. Moreover, it is neither necessary nor justified to apply an evolutionary explanation for all observed menstrual-cycle-related behavioural phenotypes" (Kiesner et al 2020 p1113).

Kiesner et al (2020) were not challenging evolutionary theory as such, rather the concern was with "(a) the lack of attention to the many other menstrual-cycle-related symptoms that may result in third-variable confounds and compromised internal validity; (b) the exclusive focus on proximity to ovulation as the driving force of cyclical changes in behaviour rather than balanced attention to both ovulation and menstruation; (c) the lack of attention to individual differences; and (d) reliance on theoretical models that fail to consider or specify pathways involving the many biological, physical, psychological, and social changes that are associated with the menstrual cycle" (p1113).

Taking these four points in more detail:

a) Ovulation and menstruation are key in the monthly cycle, but "are only two of the many physiological, psychological, and physical changes that unfold across the cycle" (Kiesner et al 2020 p1114) (eg: headaches/migraines and the consequences of these, like depressive mood, irritability, and social withdrawal).

Kiesner et al (2020) pointed out that two meta-analyses in 2014 on date preferences across the menstrual cycle included few studies that controlled for the potential confounders of these other changes.

b) There is too much of a preoccupation with proximity to ovulation in studies, and hence a downplaying of proximity to menstruation. Behaviours will vary across the whole cycle, and "choosing ovulation over menstruation as the exclusive point of reference inherently leads to a biased interpretation" (Kiesner et al 2020 p1117).

For example, "menstrual headaches may cause a decrease in some specific social behaviours during menstruation, this effect could be statistically modelled and interpreted as an increase in those social behaviours close to ovulation. However, this increase in social behaviour around ovulation would simply reflect a spurious correlation that is the inverse of the actual causal effect of the menstrual headache—occurring during menstruation" (Kiesner et al 2020 p1117).

c) There is great variety between women in their experiences, and so "individual responses to the menstrual cycle are not homogeneous and that average patterns of change across women are not likely to be meaningful" (Kiesner et al 2020 p1119).

d) It is one thing to find associations of behaviours with ovulation (or any part of the menstrual cycle), but there needs to be explanations for these findings, and the explanations should take account of the many factors involved (Kiesner et al 2020).

Kiesner et al (2020) provided an example: "the causal pathway from the menstrual cycle to changes in body-image dissatisfaction could be hypothesised to start with direct effects of reproductive steroids on diverse CNS tissues... that may result in behavioural and affective changes associated with the menstrual cycle such as food cravings, feeling out of control, anxiety, irritability, and depression... These psychological changes could then influence behaviours such as impulsive and emotional eating..., which could be reinforced and maintained by their ameliorating effects on negative affect through direct gut-to-brain signalling... These changes in eating, combined with premenstrual fluid retention..., weight gain, and abdominal heaviness/discomfort..., as well an increase in acne... may result in increased levels of body-image dissatisfaction, which has been repeatedly found to peak peri-menstrually... and which could further change social and health behaviours" (p1122).

Overall, Kiesner et al (2020) were particularly critical of the methods of researchers studying the menstrual cycle and behaviour. The authors ended: "Although we cannot infer that researchers in this area have not considered these issues, they are consistently not formally addressed. Because they represent obvious and important confounds that threaten the internal validity of research in this area, we argue that these issues must be explicitly and formally addressed at all levels, including theory development, research design, and data analysis" (Kiesner et al 2020 p1126).

8.9. APPENDIX 8A - NESTS AND WEATHER

Fruth et al (2018) reviewed 46 studies published between 2000 and 2017 on nest construction in the great apes, and the hypotheses:

i) Comfort hypothesis - This is the idea that nests evolved because they facilitated more comfortable sleep (eg: protection from wind and rain).

ii) Anti-predator hypothesis - Nests aid in protection from predators when the sleeper is vulnerable.

iii) Thermoregulation hypothesis - In cold night temperatures, nests help in maintaining warmth.

iv) Anti-pathogen hypothesis - eg: nests protect against disease carriers like mosquitoes.

Many animals make constructions for their sleep period. Great apes, for instance, build daily nests/shelters that are used for overnight sleep, and daytime rest (Stewart et al 2018).

It is suggested that there is a common great-ape ancestor who developed this behaviour, which facilitated the evolution of cognitive and technical skills in hominoids [34] (eg: Fruth and Hohmann 1996). "Nest building is complex, requiring sequential combination of branches into a secure platform in highly variable arboreal substrates. Captive individuals build higher-quality nests more efficiently if they have had exposure to experienced nest-builders early in life, indicating that learning plays an important role in the development of nest-building skills" (Stewart et al 2018 p550). Nest-building can be viewed as a form of problem-solving and of tool use (Stewart et al 2018).

As well as a place to sleep, nests may provide insulation in cold and rainy conditions. Stewart et al (2018) investigated this aspect in relation to chimpanzee

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[34] A general term covering great apes, and humans and ancestral species.

nests (figure 8.3). Data were taken from two study sites [35] in Africa in 2007-8, 2009, and 2014, and included both naturalistic observation and experiment.

In the naturalistic observations, architectural data about the nests were compared to weather conditions, while ten experimental nests were built and the temperature measured.

"All experimental nests built provided insulation with slower temperature loss within nests, than outside of nests" (Stewart et al 2018 p553). The observations showed that nest thickness, and amount of material used increased in colder conditions [36]. Wetness (based on relative humidity) also influenced nest-building. The chimpanzees at the two study sites showed some differences in nest building. The results suggested that "wild chimpanzees show flexible building techniques in response to local, overnight weather conditions in making an insulating and stable, supportive platform for sleep" (Stewart et al 2018 p549).

(Source: Yakoo1986)

Figure 8.3 - A chimpanzee sleeping nest.

In terms of the common great-ape ancestor, in the

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[35] These included forest and grassland environments.

[36] Twenty-five variables from over 200 nests were measured (eg: depth; central thickness; length), and these were reduced to eight components by factor analysis.

evolutionary past "as the climate cooled and habitat dried..., great ape nests may have been shelters to buffer apes against increasingly stressful environmental conditions, including changing climate, habitat loss, and varying predator guilds. These shelters may have ultimately aided the dispersal and survival of a branch of hominoids represented by surviving species of great apes and humans. Nests may have improved type and quantity of sleep through better thermoregulation, and a recumbent posture in a safe and secure location, which may in turn have facilitated the evolution of greater cognitive abilities" (Stewart et al 2018 p560).

In the evolution of nests and sleep in human ancestors, Samson and Nunn (2015) proposed "a positive feedback loop that merges two previously exclusive hypotheses: namely the 'sleep quality hypothesis', which assumes that improved sleep led to an increase in cognitive abilities, and the alternative 'engineering hypothesis', which assumes that the increasing cognitive performance of great apes enabled them to build nests" (Fruth et al 2018 p504).

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9. EMOTIONS

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9.2. Perceiving emotions and calls
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9.3. Horses
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9.5. Appendix 9A - Dissenters
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9.7. References

9.1. FACIAL EXPRESSIONS

It was first argued by Charles Darwin, and now it is agreed by most researchers that "forms of evolutionarily conserved 'emotion states' exist across species" (Dolensek et al 2020 p89). But studying emotions in non-humans is, for example, "hindered by a lack of rapid and precise readouts of emotion states in model organisms, such as mice" (Dolensek et al 2020 p89) (appendix 9A).

Facial expressions are one way to study emotions, and Dolensek et al (2020) reported work with mice that investigated activity in the insular cortex in the brain and stereotyped facial expressions. The mice were exposed to a selection of "emotion events" (eg: painful tail shocks; sweet sucrose; bitter quinine) while their head was fixed and electrodes had been implanted in the brain areas of interest.

Video recordings of the facial expressions were categorised by machine learning [37], as well as in terms of intensity, valence, and persistence.

Intensity of the facial expression varied with the strength of the stimulus (eg: stronger tail shock produced greater pain expression), and valence (ie: whether the experience is good or bad). For example, "[S]alt is appetitive for rodents at low concentrations but aversive at high concentrations" (Dolensek et al 2020 pp91-92). So, at low concentrations it produces a "pleasure" facial expression, but a "disgust" response at high concentrations.

Girard and Bellone (2020) commented on this work as providing "an objective analysis tool that is essential to be able to understand the neurobiological mechanisms

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[37] Girard and Bellone (2020) noted that "although it is possible for human observers to detect in animals facial movement in response to a set of sensory stimuli, it is difficult to intuitively classify the intrinsic attractiveness" (p33). Previous studies with human observers trying to "recognise emotions using facial expression in rodents are limited to a single emotion, require a long process of manual scoring, and are biased by human factors or difficult to reproduce" (Girard and Bellone 2020 p33).

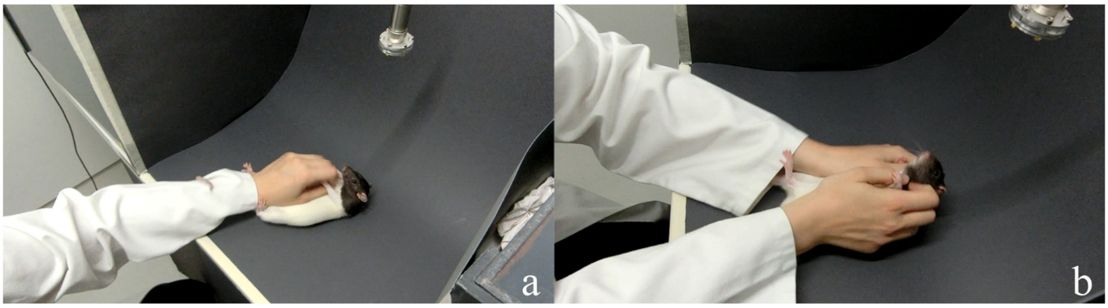
of emotions, to identify species-specific emotions, and to identify their variability across individuals. However, although facial expression often reflects a genuine emotion, humans can pose expressions even in the absence of an underlying emotion. Can animals do this too? It is also interesting to consider whether using the approach proposed by Dolensek et al will allow sufficient understanding of emotion to build robots that can read and react to human emotion to better interact with our society" (p34).

With rodents, for example, the Rat Grimace Scale (Sotocinal et al 2011) was developed to identify facial expressions in relation to pain. But the "communicative function of facial expressions in rodents is still open to debate. Rats communicate primarily through olfaction, touch, and vocalisations, and only to a minor extent through visual cues. Thus, the adaptive value of facial expressions as a means of social communication could be questioned" (Finlayson et al 2016 p2). There is some evidence that mice pay attention to each others' facial expression (Finlayson et al 2016).

"An alternative adaptive explanation for the function of facial expressions is that individuals may gain self-directed benefits from exhibiting such expressions. In the same way as expressions of fear increase sensory exposure (eg: widening of the eyes to enhance vigilance) and expressions of disgust decrease it in humans, expressions of aggression and/or fear in mice may be aimed at protecting vulnerable parts of the face (eg: tightening of eyes, flattening of ears)" (Finlayson et al 2016 p2).

Concentrating on positive emotions, Finlayson et al (2016) investigated if rats show facial expressions indicative of such emotions after tickling by an experimenter (figure 9.1). Fifteen male at a university in Switzerland were habituated to human handling and tickling. Photographs were taken of the face of the animal after a period of tickling (Positive condition). The control (or Contrast) condition was a novel room with intermittent white noise and no tickling (ie: mildly aversive).

Different aspects of the face (known as "action units" on the Rat Grimace Scale) were categorised from the photographs.



(Source: Finlayson et al 2016 figure 2)

Figure 9.1 - Tickling techniques used - (a) one-handed; (b) both hands.

The tickling appeared to produce a positive emotional state based on the rats' vocalisations. These are ultra-sonic, but with the appropriate equipment, recordings were possible, and the particular vocalisations associated with pleasure have been established (Wright et al 2010). Two "action units" were distinguished - ear colour (significantly pinker after tickling) (figure 9.2), and ear angle (wider in its tilt along the face) (figure 9.3). Other "action units" showed bo difference between conditions (eg: eyebrow angle - ie: openness of the eye).

(Source: Finlayson et al 2016 figure 7b)

Figure 9.2 - Ear colour after tickling (left) and control condition (right).

(Source: Finlayson et al 2016 figure 8)

Figure 9.3 - Ear Angle after tickling (left) and control condition (right).

9.2. PERCEIVING EMOTIONS AND CALLS

"Emotions have an adaptive value because they allow animals to respond appropriately to salient stimuli. Negative emotions enable individuals to respond appropriately to potentially life-threatening situations. Positive emotions, by contrast, guide responses to stimuli or events that enhance fitness and widen the individual cognitive and behavioural repertoire" (Baciadonna et al 2019 p1).

Studies have shown the ability to perceive the emotional state of individuals of the same species (conspecifics) and of other species (heterospecifics).

In the former case, odour or vocal cues from individual cattle, pigs, and geese, for instance, have an affect on the observer (ie: same emotion produced) (Baciadonna et al 2019).

Baciadonna et al's (2019) experiment with goats (Capra hircus), a highly social species, is an example of how the research is done. Twenty-four adults at a sanctuary in England were the participants. Three types of emotional call were played to an individual animal - food anticipation (positive, high arousal), food frustration (given when one animal has food and the other does not; negative, high arousal), and isolation (negative, low arousal). The calls were recorded previously from goats in the three situations.

Recognition of the different types of calls was tested using the habituation-dishabituation-rehabituation (HDR) paradigm. One type of call is played a number of times until the goat no longer responds (habituation), then a different call is played (dishabituation). This should produce a response if the goat can distinguish the different calls. Then the original type of call is played again (rehabituation), and there should be a response.

Four sets of calls were used:

- Food anticipation (habituation), food frustration (dishabituation), food anticipation (rehabituation);
- Food anticipation, isolation, food anticipation;
- Food frustration, food anticipation, food frustration;
- Isolation, food anticipation, isolation.

The duration of looking towards the loudspeaker was the measure of response as well as a non-invasive harness-based recording of heart rate.

The duration of looking varied during the sequence of calls suggesting that the goats could distinguish the different types of calls. Heart rate varied with the calls suggesting a perception of the emotional content.

Baciadonna et al (2019) explained: "Perceiving the emotional state of another individual through its vocalisations and being affected by those vocalisations have a strong adaptive value considering the dynamics of social organisations where, for example, group size and composition changes over time. Many social animals live under environmental conditions where individuals are not always in visual contact with one another during the day or night, and therefore, could acquire an evolutionary advantage through the discrimination of the emotional content of conspecifics' calls. Furthermore, expressing emotions using vocalisations and being able to detect and share the emotional state of a conspecific may facilitate motor coordination among the individuals in a group and strengthen social bonds and group cohesion" (pp5-6).

9.2.1. Heterospecific Call Recognition

Perception of heterospecific calls has been tested with humans and their ability to recognise the arousal (emotions) in chimpanzee vocalisations. Kamiloglu et al (2020) performed two experiments.

Experiment 1

The participants were 310 individuals recruited from the University of Amsterdam's Department of Psychology research pool. Individually, participants listened to 155 chimpanzee vocalisations (eg: pant hoot when discovering food; alarm calls; victim screams when attacked by another chimpanzee) and stated the context of the call from a choice of ten situations, rated the level of arousal of the caller (1 = very low, to 5 = very high), and the emotional valence (1 = very negative, to 5 = very positive).

Recognition of the behaviour context of the vocalisation was poor, but the participants were able to identify high arousal calls, particularly in a negative context.

It was accepted that the task was too difficult for participants with ten unfamiliar behaviour contexts. This is "a large number of options for a categorisation task. It has been suggested that even though increasing the number of alternatives in forced-choice tasks has advantages (eg: reducing the guessing rate), for a given task, there is a point at which the number of options becomes too large for participants. The present results suggest that for human listeners to be able to accurately map chimpanzee vocalisations to 10 unfamiliar behavioural contexts, participants may require additional information about the contexts, and/or information carried by other channels such as facial expressions" (Kamiloglu et al 2020 p8).

Experiment 2

The participants here were 3120 adults recruited from Amazon Mechanical Turk. They were presented with ten calls and a behaviour context in each case, and asked if the two matched ("match-to-context judgment"). Only a quarter of the calls were presented with the correct context. Scoring was a hit or a miss.

Overall, there were significantly more hits than expected by chance. The most accurately matched vocalisations were "being attacked by another chimpanzee", "being refused access to food", and finding food (not in any order).

"In general, listeners' judgments of negative behavioural contexts were more accurate than judgments of positive contexts. Similarly, high arousal vocalisations and valence were more accurately inferred from vocalisations produced in negative contexts. In particular, accuracy was especially high for highly aroused negative vocalisations, which might signal immediate, potentially dangerous situations. It has been proposed that stronger phylogenetic continuity for negative affective signals may be a result of a homologous signalling system that benefits species in dangerous contexts" (Kamiloglu et al 2020 p8).

Kamiloglu et al (2020) observed: "Given that listeners in our experiment had minimal prior exposure to chimpanzees, they are unlikely to have learned to decode chimpanzee vocalisations. Rather, accurately mapping heterospecific vocalizations to behavioural contexts linked to affective states may draw on acoustic regularities that are conserved across related species" (p8).

Acoustic features of the vocalisations were used by listeners like noisiness to match context, "while more simple acoustic features like pitch mean and pitch variation were more effective in identification of arousal and valence" (Kamiloglu et al 2020 p8). Pitch has been found to be important in human recognition of emotional content of piglet calls (Maruscakova et al 2015), and other terrestrial vertebrates (Filippi et al 2017; table 9.1).

- Filippi et al (2017) recruited three groups of students for their research (25 English speakers, 25 Mandarin speakers, and 25 German speakers). They were played ten pairs of vocalisations each from nine vertebrate species - hourglass tree frog, African bush elephant, giant panda, domestic pig, Barbary macaque, American alligator, common raven, black-capped chickadee, and human. The task was to rate the level of arousal of the caller. Half the calls were during high arousal (eg: predator threat), and half low arousal.

- The participants were correct significantly more than chance (50%) about the arousal of the caller as high or low. Not surprisingly, they were most accurate for human vocalisations. Frequency-related information of the vocalisations seemed to be used in the judgment of arousal.

Table 9.1 - Details of Filippi et al (2017).

Other studies on heterospecific call recognition include African elephants' ability to distinguish threatening and non-threatening human vocalisations (McComb et al 2014) (appendix), and Japanese sika deer following the vocalisations of Japanese macaques on discovering fruit (Koda 2012; table 9.2) (appendix 9B).

- In Southern Japan, Japanese macaques (Macaca fuscata yakui) and Japanese sika deer (Cevus nippon) live close together in high population densities. "Although arboreal fruits are attractive food resources for deer, it would be difficult for deer, as entirely terrestrial animals, to obtain them. To increase their efficiency in foraging fruits, it has recently been found that deer rely considerably on fruit falls from macaques foraging trees in the area" (Koda 2012 p31).

- Recordings of macaque food-associated calls were played to the deer, and the response of the latter were observed. Significantly more deer moved towards the tree with the speaker playing the macaque calls than when silence was playing.

- But no deer responded in nine of 20 call playback sessions, which "would suggest that the macaque food calls weakly attract deer and that deer do not actively follow the macaques. Alternatively, if deer happen to hear macaque food-associated calls in the near distance, deer may opportunistically move to the tree where the macaque group is foraging" (Koda 2012 p33).

Table 9.2 - Details of Koda (2012).

9.3. HORSES

Horses have been observed to appear "withdrawn" (or "apathetic", "unresponsive", "switched off") - ie: "to display an atypical posture (standing motionless with eyes open, stretched neck and similar height between neck and back)" (Fureix et al 2012 p2). They also have "dull eyes looking nowhere" in domestic environments (eg: Hall et al 2008).

Fureix et al (2012) explored this further, and as a possible animal model of human depression. Fifty-nine horses from three riding schools in France were observed in 2007. Each horse was observed in their box in five-minute sessions, including their posture, head movements, gaze durations, and ears movement. The responsiveness to touch, and to the sudden appearance of a human was recorded.

About one-quarter of the horses displayed at least once the withdrawn posture. These horses also showed an absence of ear and head movements, and a fixed gaze with no eye movements. They were less responsive to touch, and reacted with indifference to the human appearing. In blood samples, the "depressed" horses had lower cortisol levels. "All these characteristics present strong similarities with some aspect of the depressive states of humans and other animal models" (Fureix et al 2012 p7).

9.4. MACHINE LEARNING AND CATEGORIES

The basis of psychology has been "attempts to map measurements of the brain, body, and behavior to common-sense mental categories for cognitions, emotions, perceptions and so on. Many empirical efforts within psychological science rely on the assumption that Western folk category labels constitute the biological and psychological 'ground truth' of the human mind across cultures (eg: mapping categories such as attention, emotion, or cognition onto functional brain networks), while other efforts are more neutral in their assumptions, inferring only that the category characterises a participant's behavior (eg: rating of experience conditioned on experimenter-provided folk labels)" (Azari et al 2020 p1). But what happens if these folk or everyday categories do not map onto brain activity, physiological changes, and behaviour?

Azari et al (2020) explored this issue with reference to emotions, where that enforce strict category boundaries are traditionally imposed on data..." (p2). In particular, these researchers focused on the use of machine learning techniques which attempt to "build classifiers that can identity 'biomarkers', 'signatures', or 'fingerprints' for pre-defined mental categories" (Azari et al 2020 p2). Participants are exposed to emotion-inducing stimuli (eg: music; movies; stories) while experimenters take measurements of the brain, body, and/or behaviour. Then algorithms (machine learning) seek patterns in the data.

This assumes, in most cases, universality to emotions, but studies have not found consistent results. "For example, individual studies report patterns of ANS [autonomic nervous system] activity that distinguish one emotion category from another, but the actual patterns vary across studies for a given emotion category, even when the studies in question use the same methods and stimuli and sample from the same population of participants" (Azari et al 2020 p3). There are methodological issues that could explain the differences, including small sample sizes, or computational settings in brain imaging studies. "It is also possible that current functional brain imaging measures are insufficiently sensitive or comprehensive to identify the biomarker for a given emotion category. There may also be more than one biomarker for each category, or perhaps a single biomarker exists but multiple models capture this ground truth in different ways. But it may also be that the relationship between the presumed emotion categories, used to generate the labels for the analysis and the physiological response measured in the body or brain, are simply more complex than can be fit with a consistent relationship between the two" (Azari et al 2020 p3).

Another issue is the individual variability in an emotion. "People vary in their physical actions across instances of the same emotion category that occur in different situations (eg: when experiencing fear, a person may run away, freeze, or attack); as a consequence, instances of fear will vary in their physiological features" (Azari et al 2020 p3).

Azari et al (2020) described these concerns by re-analysis of three types of study of emotions:

i) Neuroimaging while listening to auditory stimuli, participants labelled the emotional experience as happiness, sadness or fear (Wilson-Mendenhall et al 2013). The aim was to find correlations between patterns of brain activity and these emotional labels.

ii) Self-reporting of emotional experience across fourteen days while physiological measures were recorded (eg: heart rate) (Hoemann et al 2020). The purpose was to find associations between freely labelled emotional experiences and physiological changes (eg: time between heartbeats - inter-beat interval).

iii) Participants shown movie clips and rated yes or no for emotional words (Cowen and Keltner 2017).

All the data were re-analysed by Azari et al (2020) using supervised and unsupervised machine learning. The latter involves algorithms looking for patterns without any emotional labels, while supervised machine learning uses the emotional labels to guide pattern-seeking.

Azari et al (2020) explained the hypothesis: "it is possible that the emotion category labels used in these three datasets (and most past studies of emotion categories) veridically reflect biological and psychological categories that exist in nature and are stable across contexts and individuals, and that latent emotion constructs do in fact, produce distinct, if graded, responses in brain, body, and behavior" (p10). If so, the supervised machine learning should produce more meaningful patterns in the data than unsupervised learning. The researchers did not find clear cut evidence. They stated: "our results may suggest the possibility that supervised machine learning is capable of discovering signal that is stipulated by the stimuli used to manipulate emotion, but that signal may not be sufficiently strong to be detected with unsupervised analyses alongside other real world variability in other features. This makes the accuracy of the labels critical, since they impose the viewpoint from which that structure is discovered, and thus suggests the need for careful, cross-study, sceptical interpretation of supervised results until validity of the labels can be scientifically determined" (Azari et al 2020 p10).

The implication is that emotional categories, which are Western in origin, do not adequately make sense of biological signals. "There may be substantial contextual differences, individual differences, and cultural differences in how a human brain makes biological signals meaningful when creating emotional events to guide action" (Azari et al 2020 p10).

9.5. APPENDIX 9A - DISSENTERS

The long-held view that facial expressions are a guide to our underlying emotions is challenged by "dissenters" who see these "expressions" as "tools that we use to manipulate others" (Young 2020 p45).

The traditional view is based on research in the West that focused on universal emotions, and then tested non-Western groups for support. These studies often ask participants to match a photograph of a facial expression to an emotion word (Young 2020).

Research in non-Western situations which simply asks participants to sort images of posed facial expressions finds different results (eg: Gendron et al 2014 and Himba people in Namibia).

The view of facial expressions as a means of communication, like a smile signalling to others the desire to work together, is pioneered by Alan Fridlund (eg: Crivelli and Fridlund 2018) (Young 2020).

9.5.1. Face Perception

Chang and Tsao (2017) described 2000 faces on two criteria - shape (eg: distance between eyes) and appearance (eg: complexion) - to produce fifty features. In monkeys, the response of 205 "face cells" ("face patches") in the infero-temporal cortex were found to predict the face shown. The cells appear to be responding to features of a face rather than to specific faces, though the memory regions store information to help recognise known individuals (Tsao 2019).

9.6. APPENDIX 9B - ELEPHANTS AND HUMANS

African elephants in Kenya have a history of conflict with the Maasai people, but positive interactions with the Kamba people. McComb et al (2014) played recordings in both languages from concealed loudspeakers to see the reaction of the elephants [38].

The animals were more likely to "bunch" together in defence (ie: a tight circle with the young in the centre) to the Maasai male voice than the Kamba one. "This study suggests that an animal species has adapted its natural behaviour to include humans as a dangerous predator" (Plotnik and de Waal 2014 p5072).

Other research has found a greater fear-based response to the scent and colour of clothes worn by Maasai than Kamba men (Bates et al 2007).

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[38] The researchers played 142 recordings with 47 elephant family groups.

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10. WATER

10.1. Shark mistakes
10.2. Water-hopping
10.3. Swordfish
10.4. Grey whale
10.5. Bowhead whale
10.6. Miscellaneous cetaceans
10.7. References

10.1. SHARK MISTAKES

White sharks (Carcharodon carcharias) along the California coast of the USA hunt pinnipeds (eg: seals), but they also mistarget sea otter (Enhydra lutris nercis) (ie: exploratory bites but not consumed). However, the wounds may lead to death of the otters.

Moxley et al (2019) investigated this relationship between sharks and sea otters with shark tagging data, and details of strandings of otters off the central Californian coast (eg: Farallon Islands off San Francisco) (for 1997 to 2013).

The attacks on sea otters peaked when sharks returned from the distant ocean in preparation for the increased seal population in the area [39]. At this time, the sharks were "resource depleted", and so attacked any "seal-like" shape for food. This period of vulnerability for otters expanded from two to eight months of the year during the study period with ecosystem changes (eg: ocean warming).

10.2. WATER-HOPPING

There are some fish species that can launch themselves into the air from the water. For example, the one-metre silver arowana (Osteoglossum bicirrhosum) [40] of the Amazon can capture small birds and snakes this way, while other fish do it to avoid predators, like the African butterfly fish (Pantodon buchholzi) [41] which launches vertically into the air ("a vertical startle response") (Wicaksono et al 2020).

Wicaksono et al (2020) reported the case of dusky-gilled mudskippers (Periophthalmus variabilis) [42] hopping on the water surface to reach trees or rocks. These fish are part-terrestrial, part-aquatic, and were filmed in

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[39] The preferred prey in this case is immature elephant seals.

[40] Details at https://www.fishbase.de/summary/6234.

[41] Details at https://www.fishbase.se/summary/Pantodon-buchholzi.html.

[42] Details at https://www.fishbase.de/summary/65362.

the mangrove swamps in Indonesia.

The researchers summed up their fieldwork thus: "During our daylight observations of P. variabilis water-hopping, we noted that these mudskippers would generally avoid complete submergence into water, even if being chased. We did note nevertheless, a few instances where mudskippers would enter their burrows after hopping events. From our observations, we note that the mudskippers appeared to use water-hopping as a means of coming closer to their burrows when threatened. In the vast majority of water-hopping events, mudskippers would begin on a solid substrate and end on a solid substrate, hopping upon the water surface in between" (Wicaksono et al 2020 p3).

10.3. SWORDFISH

Inter-specific aggression does occur in some fish species (eg: swordfish) (Jambura et al 2020).

In April 2020 a dead female big-eye thresher shark (Alopias superciliosus) was reported on social media on the Libyan coast [43]. Jambura et al (2020) analysed the videos and photographs posted, which showed the tip of a rostrum of a swordfish (Xiphias gladius) stuck in the fin.

The researchers proposed that "based on the location, the length and the angle of the impaling rostral portion, it can be that the shark was injured at or near the vertebral column and the branchial apparatus, probably severely injuring branchial nerves, branchial arteries and gill arches" (pp2-3). But was this a deliberate attack by a swordfish or an accidental collision, Jambura et al (2020) asked?

Intentional impalement has been reported before, but the breaking of the rostrum could seriously disadvantage the swordfish (eg: in swimming and feeding functions). However, individuals with damaged, malformed, or missing rostra have been observed in apparently good physical shape, "leaving room for speculation if swordfish experience a trade-off between averting a threat (eg: sharks) and the potential impairment of high-speed locomotion" (Jambura et al 2020 p3).

Jambura et al (2020) hypothesised that competition for resources between swordfishes and sharks meant that either explanation is possible. "This fatal injury might have been the result of an accidental collision, eg: while feeding on the same prey resource. However, the potential for the impalement to be a result from a

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[43] Pictures and details at, for example, https://www.sciencealert.com/a-weird-sword-was-found-embedded-in-a-dead-thresher-shark.

directed attack against the shark to drive a competitor away from this resource cannot be excluded either" (Jambura et al 2020 p4).

10.4. GREY WHALE

The oceanic migration of whales is little studied, mainly because of practical problems. So, it is not clear about the cues used migrating, for instance (Granger et al 2020).

Strandings may help, particularly where individuals were not ill or injured, and resumed migration after rescue. Granger et al (2020) explained: "It is therefore possible that a portion of these animals stranded due to navigational errors. Although many factors impact strandings (eg: naval mid-frequency sonar, disease, etc), here we focus on whether strandings can be used to study the potential for magnetoreception in migratory whales" (pR155).

Vanselow et al (2017), for example, had reported a positive association between strandings of sperm whales and sunspot counts (which is a sign of solar storms and of the release of high-energy particles that could disrupt magnetic orientation).

Granger et al (2020) collected data for over thirty years on the grey whale (Eschrichtius robustus) (n = 186 strandings). The researchers concentrated on two variables affected by solar storms - radio frequency (RF) noise, and displacements in the Earth's magnetic field (measured by the Ap-index). Strandings were associated with high RF noise only. "These results are consistent with the hypothesis of magnetoreception in this species, and tentatively suggest that the mechanism for the relationship between solar activity and live strandings is a disruption of the magnetoreception sense, rather than distortion of the geomagnetic field itself. While these results are consistent with the radical-pair hypothesis of magnetoreception, which is predicted to be disrupted by RF noise, they do not preclude other possible receptors, such as one based on magnetite. This research is not conclusive evidence for magnetoreception in this species, and further research is still necessary to determine the mechanism for the increase in strandings under high RF-noise" (Granger et al 2020 pR156).

10.5. BOWHEAD WHALE

The bowhead whale (Balaena mysticetus) was hunted nearly to extinction in the past, but the number now in the Arctic Circle is not known. Ship-based surveys and sightings suggest a few individuals, while acoustic monitoring has recorded "abundant singing taking place 24 hours per day in the winter months" (Kovacs et al 2020 p1).

Vacquie-Garcia et al (2017) estimated numbers in the low hundreds in the Norwegian High Arctic in late summer 2015 based on helicopter observations. Thirteen whales were tagged, and Kovacs et al (2020) analysed six months worth of data. They summed up the findings: "Despite their reduced abundance, Spitsbergen’s bowhead whales occupy much of their historical range, stretching across the northern Barents Region from East Greenland eastward to Franz Josef Land. Unlike larger bowhead populations to the west, they do not migrate in a classical sense, but rather disperse from wintering grounds in the northernmost parts of their range during spring, returning northward again in autumn, a pattern opposite in terms of directionality compared to other Arctic bowhead whale populations. The extreme affiliation of this population with cold, ice-filled waters is a concern given ongoing climate warming and concomitant rapid sea ice habitat loss" (Kovacs et al 2020 p1).

10.6. MISCELLANEOUS CETACEANS

Cetaceans and primates include species with highly evolved brains. "Cetacean brains are thought to have numerous features that deviate from general mammalian trends, including a thin and highly laminated cortex, extreme gyrification, low neuron density but high synaptic density, unique neuronal cell types, and small hippocampi that lack adult neurogenesis" (Muller and Montgomery 2019 p1419).

Key to primate brain expansion is "the co-evolution and co-ordinated expansion of the cortico-cerebellar network" (Muller and Montgomery 2019 p1419) (ie: the development of the cerebellum (CB) and the cerebral cortex (CX) relative to the rest of the brain (ROB)).

What about cortico-cerebellar co-evolution in cetaceans? Ridgway et al (2017) collected a dataset on the brain structure of eighteen cetacean species, which Muller and Montgomery (2019) analysed, and compared with terrestrial mammals.

Despite certain unique features, cetacean whole brain expansion was linked to cortico-cerebellar expansion. Muller and Montgomery (2019) explained: "Across cetaceans, we find no evidence of a simple linear relationship between either cerebrum and cerebellum size and the complexity of social ecology or acoustic communication, but do find evidence that their expansion may be associated with dietary breadth. In addition, our results suggest that major increases in both cerebrum and cerebellum size occurred early in cetacean evolution, prior to the origin of the major extant clades [44], and predate the evolution of echolocation" (p1418).

Belugas (or white whales) (Dolphinapterus leucus) and narwhals (Monodon monoceros) are cetaceans found in the Arctic waters all year-round. They diverged around 5 - 1.25 million years ago (Skovrind et al 2019).

They are similar-sized, and show similar breeding and nursing behaviours, but differ in prey selection and diving capabilities. Belugas feed on fish at 0-500 metres depth, while narwhals dive deeper, feeding on fish and squids (Skovrind et al 2019).

In 1990 a skull was found in West Greenland that appeared to be a beluga/narwhal hybrid, which Skovrind et al (2019) recently confirmed with genome-wide DNA analysis. The mother was a narwhal and the father a beluga.

Skovrind et al (2019) observed: "Mating strategies of belugas and narwhals are not well understood, reflecting the logistical challenges associated with studying the behaviour of Arctic marine endemics; mating takes place in spring, when the whales are particularly difficult to access due to sea ice break up. However, the existence of a beluga/narwhal hybrid indicates that the two species can mate and produce viable offspring" (p8).

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[44] A clade is a group of organisms with a common ancestor.

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11. FROGS

11.1. Polymorphism
11.2. Batesian mimicry
11.3. Nests
11.4. References

11.1. POLYMORPHISM

Within a species, there may be many different types of individuals in a population (known as polymorphisms), and this can provide a step to a new species (speciation) (Verzijden 2019).

Yang et al (2019) studied the strawberry poison frog (Oophaga pumilio), a brightly coloured small frog in Central America. The bright coloured skin warns predators that the frog is toxic. But there are many different skin colours. If females had a preference for a particular skin colour among males, then the most popular colour would dominate.

So polymorphism in skin colour is driven by something other than female choosiness. Yang et al (2019) showed that offspring prefer to mate with individuals with the same skin colour as their mother (established through sexual imprinting).

Yang et al (2019) studied tadpoles in three conditions using three skin colours - (i) raised by biological parents (both same colour), (ii) raised by biological parents (different colours), or (iii) foster parents who were different coloured to the tadpole's parents. "For all three scenarios, when the female tadpoles became adults, female offspring preferred to mate with males of the same colour as the mother that had reared them" (Verzijden 2019 p39).

male offspring showed greater territorial aggression towards males of the same colour as the mother who had reared them.

Verzijden (2019) explained the situation: "If a male is the same colour as a female's mother, the probability that the female will mate with the male is boosted. However, when that colour becomes the most common type in the population, such males incur a survival penalty by being subject to competitive aggression from other males of the same colour. This aggression could explain how an alternative rare colour could persist in a population because, compared with males of the common colour, males of the rare colour would instead spend less time and energy on territorial defence, and presumably expend this energy and time on attracting females, increasing their chances of mating" (p39). This is known as the "rare-male advantage" (Seehausen and Schluter 2004).

But a variety of skin colours could be a disadvantage as predators may only recognise certain colours as toxic. This means that predators could weed out rare colours. However, Cummings and Crothers (2013) proposed that "when populations are sufficiently toxic and conspicuous, predators will be able to generalise across such bright colours and recognise them as being toxic" (Verzijden 2019 p39).

Verzijden (2019) ended: "The mechanisms that Yang and colleagues reveal to be acting in O. pumilio populations show how intricately natural and sexual selection affect processes that might drive speciation, and indicate that neither process can necessarily be considered separately. In this frog species, imprinting inextricably links both female mate preferences and interactions between males, ensuring that the prevalence of these imprinted behaviours tracks extremely closely to the frequency of the particular parental colour form in the population. Previous work has shown that sexual imprinting favours leading a population on a path towards reproductive isolation [Verzijden et al 2012]. The evidence obtained by Yang and colleagues now shows how imprinting can also affect intrasexual aggression and might help to maintain polymorphisms, thereby giving an extra boost for conditions that favour speciation" (p39).

11.2. BATESIAN MIMICRY

"Batesian mimicry" (Bates 1862) is "when an innocuous organism imitates or 'plagiarises' [Pasteur 1982] a dangerous or toxic one to protect itself from predators" (Vaughan et al 2019 p1853). There are three elements of this process (Pasteur 1982) - the model (the organism being imitated), the mimic (the organism that copies the model), and the dupe (the organism being deceived) (Vaughan et al 2019).

The model will usually be noxious to predators, and so the mimic gains an obvious benefit from copying (eg: non-venomous snakes mimicking venomous species). "Some caterpillars, legless lizards, and even birds are capable of imitating venomous snake appearance and behaviour" (Vaughan et al 2019 p1854).

Vaughan et al (2019) reported what they believed was the first case of an anuran mimicking a venomous snake - the Congolese giant toad (Sclerophrys channingi) mimicking the Gaboon viper (Bitis gabonica). The body shape and colouration of the toad give the appearance of the head of the viper, though it is "not an exact match" (Vaughan et al 2019).

If the model is highly noxious, there may be imperfect mimicry ("lower mimetic fidelity"; Rodriguez et al 2014), "at least from a human perspective... "An organism that seems to be a poor mimic according to human inspection may actually be a good mimic from the perspective of its would-be predator..., especially for predators that vary in their spectral sensitivity" (Vaughan et al 2019 p1862).

The possible explanations for imperfect mimicry include (Vaughan et al 2019):

i) The model is highly numerous and noxious, and the model's predators have poor discrimination abilities.

ii) There is plenty of alternative prey to the model.

iii) A "'breakdown' in mimicry - a greater number of poor mimics when the mimic species' abundance increases" (Vaughan et al 2019 p1862).

11.3. NESTS

The Goliath frog (Conraua goliath), found in Cameroon and Equatorial Guinea, is the largest living species of frog, but "astonishingly few facts have become known about its biology" (Schafer et al 2019 p1263).

In early 2018, Schafer et al (2019) set out along the Mpoula River in Cameroon to rectify this lack of knowledge. Nineteen nests were found and observed with time-lapse cameras (taking pictures every 20 seconds).

Three types of nests were classified - rock pools cleared of detritus by the frogs (type 1), existing washouts at the riverbank that were cleared and expanded (type 2), and depressions dug into the gravel riverbanks by the frogs (type 3) [45].

The male "constructs" the nest while the female waits nearby. "Once the nest is finished, the male whistles to attract the female, which then is grasped by the male and eggs are deposited. Afterwards the female would guard the nest and subsequently open the nest towards the river" (Schafer et al 2019 p1272).

Type 1 nests were the "easiest" to "construct", but least reliable (eg: washing out of the nest by river

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[45] "Digging out a nest that exceeds 1 m in diameter and 10 cm in depth, by moving coarse gravel and stones of several kilograms, is a serious physical task, and suggest a potential explanation for why Goliath frogs are among the largest frogs in the world. Other frog species that are known to conduct arduous labour when preparing spawning sites are as well at the upper limits of anuran body size range. Examples are male African Bullfrogs (Pyxicephalus adspersus) which guard tadpoles and are digging channels to allow tadpoles to escape drying pools... or Gladiator Frogs (Hypsiboas rosenbergi)... and the Bornean Giant River Frog (Limnonectes leporinus...) that construct nests" (Schafer et al 2019 p1274).

overflows) (Schafer et al 2019). But types 2 and 3 nests were "less likely to be over-flooded, but instead have a higher risk of drying up during periods of dropping water levels. In addition, they need much effort from the frogs to be established" (Schafer et al 2019 p1274).

Schafer et al (2019) concluded that "the use of different nest types thus might reflect trade-offs between availability of sites, construction costs and survival probabilities of the offspring" (p1274).

This is evidence of parental care in both the construction of a nest, and in the guarding of eggs and tadpoles. Nest construction is not common in frogs, particularly African species.

"Constructing (nest types 2 and 3) or modifying (types 1 and 2) suitable nest sites may thus allow the frogs to prolong the possible breeding season and increase the number of breeding sites that match their demands, eg: concerning water presence and predator absence" (Schafer et al 2019 pp1273-1274).

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12. FLIERS AND INSECTS

12.1. Swift ants
12.2. Pollinators
12.3. Beetles
12.4. Wasps and transitive inference
12.5. Honeybees and lateral bias
12.6. Mosquitoes
12.7. Gulls and gaze aversion
12.8. Birds and ecosystem roles
12.9. Bird brain
12.10. References

12.1. SWIFT ANTS

Some species survive by exploiting a niche, as in the Saharan silver ant (Cataglyphis bombycina) which forages in the midday sun ("thermophilic scavenger") while predators and competitors have retreated into burrows. "To exploit this foraging niche, silver ants need to withstand the extremely hot and dry desert environment. During the hottest hours of the day, the surface temperature of the Saharan sand may easily exceed 60°C... and desiccation stress reaches its maximum with very high water vapour saturation deficits... Food density is low and long distances may have to be covered during foraging, with shady resting places absent or far apart because of sparse vegetation and mostly blue sky. Moreover, the fluid granular sand medium may impede locomotion and demands considerable energy to cross" (Pfeffer et al 2019 p1).

The ants have evolved three sets of traits to survive these challenges (Pfeffer et al 2019):

i) Morphological (changes to external body) - eg: triangularly shaped hairs which have thermoregulatory effects.

ii) Physiological (changes to internal body) - eg: "a discontinuous ventilation cycle that reduces respiratory water loss" (Pfeffer et al 2019).

iii) Behavioural - eg: faster speed of movement to lessen the time in the heat.

Pfeffer et al (2019) recorded the running speeds of equivalent to 108 body lengths per second in observations in the field (Tunisian desert) and in the laboratory (Germany) [46]. Analysing the movements, these researchers

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[46] Two other running animals have been recorded faster in relative terms - an Australian tiger beetle (171 body lengths per second) and a Californian coastal mite (377 body lengths per second) (Pfeffer et

observed a "combination of high stride frequencies, short stance phases and fast swing movements in achieving high running speeds, together with the high synchrony of the legs in a tripod" (ie: 3 legs on ground at once) (Pfeffer et al 2019 p11).

12.2. POLLINATORS

The decline of bees and other diurnal (daytime) insect pollinators has raised concerns about the impact on insect-pollinated crop yields of human foods. Walton et al (2020) highlighted the neglected role of nocturnal and crepuscular (twilight - dawn and dusk) insect pollinators (eg: moths) [47].

Data were collected in fields in Norfolk in March-October (growing season) 2016 and 2017. Pollinating invertebrates were sampled in three ways:

- Light traps for moths at night (once a month).
- Thirty-second time-lapse photographs for diurnal pollinators (for one day per month).
- Thirty-minute random visual surveys by the researchers.

One hundred and three species were found to be nocturnal pollinators for 47 insect-pollinated plant species. "Solitary bees, wasps, syrphids [hoverflies] and butterflies formed a network of 76 pollinators, with 45 plant species visited by 632 individuals, while 11 species of social Apidae bees... comprising 1548 individuals visited 46 plant species" (Walton et al 2020 p4).

Walton et al (2020) summed up: "Acknowledging that neither flower visitation nor pollen presence on pollinators' bodies represent direct proof of pollination, our observations strongly suggest that nocturnal moths are influential components of wild plant-pollinator networks in agro-ecosystems. Therefore, moths may provide additional important resilience to pollination networks, potentially counter-balancing ongoing diurnal pollinator declines" (p4).

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al 2019).

[47] Pollination of one of five crucial roles for insects in ecosystems (Kolbert 2020). The others are as food (being a the bottom of the food chain), decomposers (ie: waste eaters), pest-controllers (ie: predatory insects feeding on crop-threatening pests), and as soil engineers (eg: termites, ants) (Kolbert 2020).

12.3. BEETLES

Sexually antagonistic selection is "an evolutionary tug-of-war between males and females over optimal trait values" (Harano et al 2010 p2036). In the case of shared traits between males and females, "selection in one sex can impede the evolution of the character toward the fitness optima of the other sex" (Harano et al 2010 p2036). This is called "intra-locus sexual conflict".

This can be seen in selectively bred populations as with Harano et al's (2010) work with broad-horned flour beetles (Gnatocerus cornutus). Males have enlarged mandibles used in male-male fights and these were the focus of the research.

Three separate populations of beetles were bred - large male mandibles (L), small mandibles (S), and controls with no selection (C) - for twelve generations.

Males from the "L" population had greater mating success than the other two groups (ie: females were more likely to copulate with them) (figure 12.1). "Thus, larger mandibles increase male fighting and mating success, and, consistent with inferences based on the derived nature of the exaggerated male mandibles (selection has favoured larger male mandibles...), males with larger mandibles have higher fitness" (Harano et al 2010 pp2036-2037).

But female fitness was lower in the "L" population compared to the other two (as measured by lifetime fecundity - ie: volume of eggs laid). "This is because mandible development changes genetically correlated characters" (Harano et al 2010 p2036).

Intra-locus sexual conflict in this species relates to the genes that control mandible growth and other characteristics, and what is advantageous to males is at the expense of females.

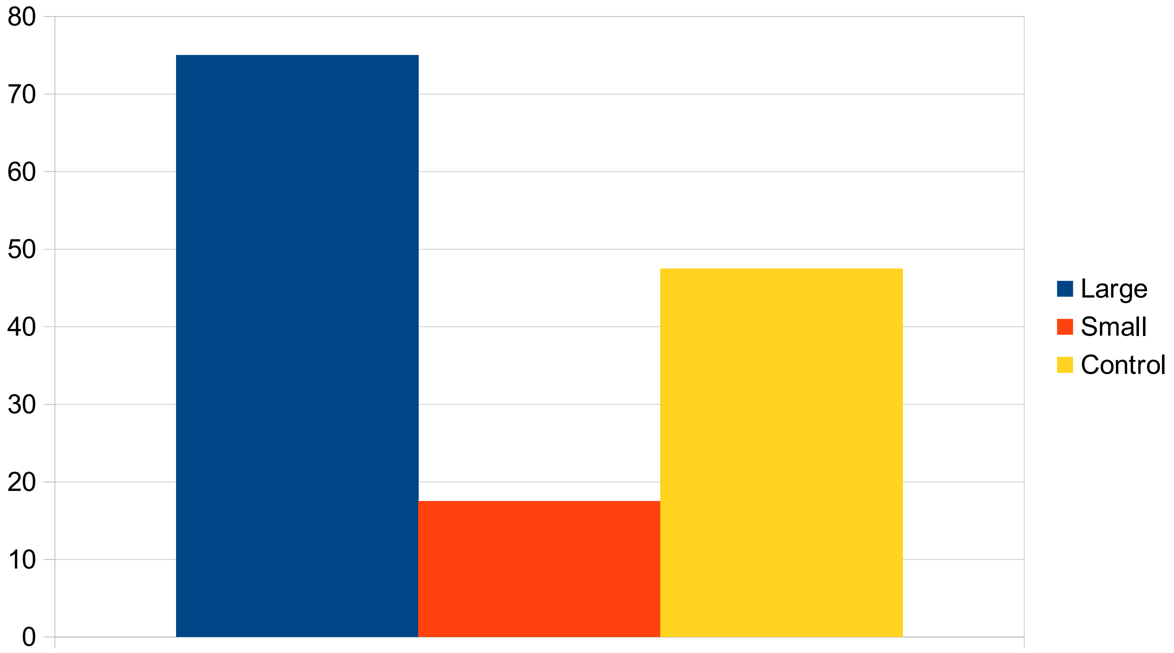

Figure 12.1 - Males (%) who secured copulation based on population.

12.4. WASPS AND TRANSITIVE INFERENCE

Transitive inference (TI) is "a form of logical reasoning that involves using known relationships to infer unknown relationships (A>B; B>C; then A>C)" (Tibbetts et al 2019 p1).

Species with complex social behaviour have the capacity for TI, which less social species do not. For example, the social pinyon jay is a highly social bird and shows and TI abilities, while the less social Western scrub-jay does not (Bond et al 2003).

In terms of invertebrates, the honeybee is the only one tested (by Benard and Giurfa 2004) and they did not make TIs (Tibbetts et al 2019). The reasons may be that "their small nervous system imposes cognitive constraints that limit the capacity for this type of reasoning. Honeybee brains have approximately one million neurons. This is tiny compared with 85 billion neurons in the human brain or 1 billion neurons in some birds. Alternatively, honeybees may not perform TI because this ability is not useful in honeybee societies" (Tibbetts et al 2019 p1).

But Tibbetts et al (2019) found in their research that the European paper wasp (Polistes dominula) and the Metricus paper wasp (Polistes metricus), with a similar nervous system size as honeybees, did make TIs. "Although honeybees live in large social groups, worker bees do not reproduce or form dominance hierarchies. Instead, workers use group-level recognition and self-organisation to produce apparently complex behaviour with little individual cognitive investment... [But] Polistes often live in co-operative societies where nest-founding queens compete to form linear dominance hierarchies. In the early spring, Polistes nest-founding queens compete with many rivals on and off nests before settling down in stable, hierarchical groups. A wasp's rank in the hierarchy determines shares of reproduction, work and food" (Tibbetts et al 2019 p1) [48].

The wasps were trained using the five-element training procedure. This involved five colours (labelled A-E), and the ability to discriminate four pairs (where one of the pair is associated with an electric shock). The aim was to train an implicit hierarchy of the colours. In each case of training, the "lower" colour was paired with an electric shock (eg: A (no shock)/B (shock) or B (no shock)/C (shock)). The testing used novel pairs, like B/D and A/E. "If wasps organise the trained stimuli into the implicit hierarchy A>B>C>D>E and use TI to choose between untrained pairs, they will choose B more frequently than D and A more frequently than E" (Tibbetts et al 2019 p2).

This was found. When tested with novel pairs, wasps chose the "higher" colour significantly more often than expected by chance. "Choice" involved deciding which end of an arena to move towards when there was a different colour at each end.

Tibbetts et al (2019) ended: "This study illustrates that paper wasps naturally build and manipulate an implicit hierarchy, but it does not test the precise mechanisms that underlie this ability" (p4).

12.5. HONEYBEES AND LATERAL BIAS

A "lateral bias" is a preference to move in one direction over another (ie: rightward or leftward). "Such biases may result from evolutionary constraints, or selective pressures, and often exert a significant and detectable influence upon behaviour" (O'Shea-Wheller 2019 p1).

O'Shea-Wheller (2019) studied the Italian honeybee (Apis mellifera ligustica) at a US university in specially made hives. Bees were presented with a choice of right or left passages in their hive, and the direction chosen by 180 individuals was recorded.

In an opening with no forced choice, the bees were significantly more likely to turn right than left, but

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[48] Note that European paper wasps live in larger co-operative nests than Metricus wasps (Tibbetts et al 2019).

when forced to choose between two passages, there was no significant preference.

The right turn in an open area fits with a right antenna preference "used in short-term memory, pheromone detection and social interaction, ostensibly owing to its greater density of olfactory sensilla. Consequently, it follows that when investigating an open cavity — that may hold both the threat of predation and promise of sociality — a right turn is preferable to a left one, as in this way workers can acquire information about their environment with greater fidelity. As such, over time, the adaptive advantages of this may have led to the development of a conserved behavioural heuristic, in which workers preferentially turn right when entering open and dark spaces" (O'Shea-Wheller 2019 pp3-4).

But in the forced choice situation,
"the utility of increased olfactory perception is likely outweighed by the navigational benefits of wall-following" (O'Shea-Wheller 2019 p4).

12.6. MOSQUITOES

A few mosquito species are responsible for the majority of mosquito-borne human illnesses, and these species are specialists (ie: biting only humans compared to generalist species that bite any vertebrates available).

"Why might mosquitoes specialise in biting humans? Most researchers speculate that human-biting would have posed no particular advantage to mosquitoes before the development of agriculture and dense, sedentary human societies approximately 10,000 years ago. After this time, abundant humans living together might have provided an easy and reliable resource. Genomic data are consistent with the idea that key human specialist taxa evolved within this time frame" (Rose et al 2020 p3570).

Concentrating on the yellow fever mosquito (Aedas aegypti) collected from 27 locations in sub-Saharan Africa, Rose et al (2020) found that these mosquitoes' preference for humans was linked to their location (ie: town or forest). Through genetic analysis and modelling, the researchers presented a picture of hot dry seaons driving the mosquitoes to lay eggs in human-stored water, which, in time, evolved into human specialisation (eg: genes related to identification of human odour). Add to that increasing human population density in Africa.

12.7. GAZE AVERSION

Herring gulls (Larus argentatus) are increasing in urban areas as "the traditional nesting sites of cliffs and islets have been exchanged for roofs, and marine prey is sometimes largely substituted with anthropogenic food" (Goumas et al 2019 p1). This leads to conflict with humans, particularly in the case of kleptoparasitism ("food-snatching behaviour").

One strategy for people is to use the gull's "gaze aversion" (ie: "the tendency to show a fearful response towards being watched, characterised by avoidance or a slower approach towards a desired object or location"; Goumas et al 2019 p2).

Goumas et al (2019) placed fried potato chips in a transparent bag on the ground in the presence of gulls in coastal towns in Cornwall, and stood 1.5 metres away. In the "looking at" condition, a researcher gazed towards the eyes of a gull approaching the food, but did not make eye contact in the "looking away" condition. Each trial lasted five minutes in this repeated measures-designed experiment. Goumas et al (2019) explained how the experiment worked in practice: "We randomly assigned individuals to receive Looking At or Looking Away first, and trial order was counter-balanced across individuals. Second trials commenced 180 s after the completion of the first trial to allow normal behaviour to resume. During this inter-trial interval, we tracked the gull using peripheral vision and concealed the food. Trials in which gulls went out of sight were excluded from the analysis" (p2).

Complete data were collected on nineteen gulls (out of 74 attempted to test). The gulls took significantly longer to approach the food in the "looking at" condition. The median difference was 21 seconds. "This demonstrates that gulls use behavioural cues from humans when making foraging decisions in urban environments, and that they find human gaze aversive" (Goumas et al 2019 p3).

12.8. BIRDS AND ECOSYSTEM ROLES

Animals play different roles in ecosystems, like as pollinators of plants, but how to quantify the role? Simply, an animal may play a single role or multiple (Pigot et al 2020). Their role(s) will link to the evolution of the body and behaviours.

Pigot et al (2020) concentrated on birds, whose relationship with plants can be divided into:

i) Primary consumers - directly eat plants:

- Aquatic herbivores
- Terrestrial herbivores

- Nectarivores
- Frugivores (fruit-eaters)
- Granivores (seed-eaters).

ii) Secondary and tertiary consumers - hunt animals:

- Aquatic carnivores
- Terrestrial carnivores
- Either vertivores (eat vertebrates) and/or invertivores (invertebrates)

iii) Omnivores - eat plant and/or animals

iv) Scavengers - eat dead animals.

Terrestrial foragers use seven different "niches" - vegetation; bark; aerial; ground; sally to surface (eg: move within tree); sally to air; sally to surface (Pigot et al 2020).

Aquatic foragers use six different "niches" - aquatic ground (ie: stand on land and put head in water); aquatic perch; aquatic aerial; aquatic surface; aquatic plunge; aquatic dive (Pigot et al 2020).

The differences in role/niches can be seen, for example, in the evolution of the beak - its size, length vs size, and width vs depth. Put simply, the beak of a terrestrial carnivore will have evolved differently to a nectarivore, say.

12.9. BIRD BRAIN

The bird brain tends to lack the layering on the surface which is the cerebral cortex in mammals, and thus it was assumed that birds had limited cognitive abilities. But work with corvids, like ravens, has shown them to be as cognitively capable as monkeys and great apes in some respects (Herculano-Houzel 2020).

The bird brain is different, and it is the pallium that is important. "In both birds and mammals, the pallium is the population of neurons that are not a necessary part of the most fundamental circuits that operate the body. But because the pallium receives copies, through the thalamus, of all that goes on elsewhere, these pallial neurons create new associations that endow animal behaviour with flexibility and complexity" (Herculano-Houzel 2020 p1567) [49].

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[49] See comparative diagram at https://www.frontiersin.org/files/Articles/20259/fnevo-04-00012-HTML/image_m/fnevo-04-00012-g004.jpg (Petkov and Jarvis 2012 figure 4).

"Mammals and birds share a common ancestor that lived ~320 million years ago. Since then, this ancestor's dorsal pallium has developed into the cerebral cortex in the mammalian lineage... In birds, the dorsal pallium developed into a nuclear structure called the hyperpallium (also called the Wulst, comprising somatosensory and visual components)" (Stacho et al 2020 p1).

Two new studies help in understanding the differences:

a) Stacho et al (2020) - Imaging of the pigeon and owl brain found "a hitherto unknown neuroarchitecture", which appears to parallel the mammalian neocortex in the organisation of fibres and neurons.

"If the bird pallium as a whole is organised just like the mammalian pallium, then it follows that the part of the bird pallium that is demonstrably functionally connected like the mammalian prefrontal pallium (the nidopallium caudolaterale) should also function like it" (Herculano-Houzel 2020 p1568).

b) Nieder et al (2020) - This study showed that "single-neuron responses in the pallial endbrain of crows performing a visual detection task correlate with the birds' perception about stimulus presence or absence and argue that this is an empirical marker of avian consciousness" (p1626).

Two carrion crows (Corvus corone) were trained to respond to the presence or absence of visual stimuli, while neuronal activity was recorded. The pattern of activity was distinguished for particular responses, and it was then possible to predict the crows' response. The pattern "develops over the time lapse of 1 to 2 s between the stimulus disappearing and the animal reporting what it perceived by pecking at a screen either for 'yes, there was a stimulus' or for 'no, there was no stimulus'..." (Herculano-Houzel 2020 p1568).

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13. MAMMALS

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13.1. NAKED MOLE-RATS

Naked mole-rats (Heterocephalus glaber) (figure 13.1) are eusocial mammals that live in colonies (or families) of up to 300 workers with a single breeding pair (Braude et al 2020).

(Source: Momotarou2012)

Figure 13.1 - Stuffed museum specimen of naked mole-rat.

These colonies are highly xenophobic, and laboratory observations have demonstrated that "naked mole-rats can discriminate foreign adults, which they will attack..., but will accept nursing pups introduced into their burrows from foreign colonies" (Braude et al 2020 p1).

Braude et al (2020) investigated this behaviour in long-term observed naked mole-rat colonies in Meru National Park, Kenya. The researchers found that "26 colonies expanded their tunnels into burrows that were known to have been occupied by neighbouring colonies in prior years" (Braude et al 2020 p2). Invasion was directly observed in four cases in the early 1990s, while genetic fingerprinting allowed indirect observation subsequently. As a colony is highly genetically related (but not inbred as falsely assumed; Braude et al 2020), individuals from another colony will be distinguishable.

The kidnapped unweaned pups from other colonies "became non-reproductive workers and hence their life effort would be categorised as slavery, in the same sense as slave-making ants" (Braude et al 2020 p3).

Braude et al (2020) argued that fear of invasion and intergroup aggression between colonies "may be a strong selective pressure for group living and extreme colony size" (p1).

13.2. LIONS

Vocal calls are used by many mammals to signal individual identity (eg: frequency differences). "In order to assess animal vocal individuality, acoustic features must first be extracted from the call recordings. Although this can be done automatically using state of the art deep learning techniques..., acoustic features are often extracted manually, whereby simple summary variables (eg: min, max and mean) associated with the fundamental frequency and the harmonics are calculated" (Wijers et al 2020 p2).

Wijers et al (2020) used an algorithm to learn acoustic features of African lion roars for the purpose of individual identity. "A single roar is typically delivered in a bout consisting of one or two soft moans followed by several full-throated roars and a terminating sequence of short grunts... The low fundamental frequency of the roar can be attributed to the long and heavy vocal folds, characteristic of the species' vocal anatomy" (Wijers et al 2020 p3).

It is known that roars carry information about an individual from playback experiments. For example, adult females can distinguish between the roars of familiar, resident males and unfamiliar ones. While calls that do not match an individual produce a strong response in the listener (Wijer et al 2020).

Wijer et al (2020) collected recordings of roars in Zimbabwe from eight lions (78 usable roars). The algorithm correctly identified individuals over 90% of the time based on the fundamental frequency contour (eg: maximum, minimum and mean Hz).

13.3. DOGS AND PERSONALITY

Human personality changes across the lifespan through maturation "a near-universal pattern" - eg: becoming more conscientious, agreeable and emotionally stable), and in response to life events (Turcsan et al 2020).

Turcsan et al (2020) investigated this topic for dogs. The participants were over 200 Border collies and their owners in Austria. They were tested with the "Vienna Dog Personality Test" (VIDOPET) and retested four years later. This is a set of fifteen sub-tests which are videotaped and scored for seventy behaviour variables. For example, the "obedience test" where the owner gives four basic commands (eg: sit) to the dog while the experimenter distracts the dog with rustling noises. Five trait dimensions were produced from the seventy variables - Sociability-obedience, Activity-independence, Novelty seeking, Problem orientation, and Frustration tolerance (eg: a large piece of sausage on a string in front of the dog).

The main personality changes were:

a) Activity-independence declined with age (eg: independent exploration of the room).

b) Novelty seeking declined in middle age (ie: >3-6 years old) (eg: interest in new objects). It is possible that this decline was due to familiarity with the test situation (Turcsan et al 2020).

c) Problem orientation increased until middle age (ie: the ability to solve problems).

d) Individual differences - Four dogs showed different patterns to the majority.

The personality dimensions are dependent on the tests used. For example, Svartberg et al (2005) developed the "Dog Mentality Assessment", which included more fear-evoking situations, and they noted the dimension of curiosity-fearlessness.

Turcsan et al (2020) admitted that "although the VIDOPET attempted to measure a broad range of personality traits in pet dogs, it was not suitable to detect individual variability in two common personality traits, fearfulness and aggression. Due to ethical and safety reasons only one subtest addressed the dogs’ fearfulness and propensity to display aggression, and we also excluded overly shy dogs from the sample. If age-related changes in these particular traits are of interest in future studies, it may be necessary to include additional subtests, as well as to explore a more diverse sample of pet dogs" (p10).

13.4. SYNTACTIC COMPREHENSION

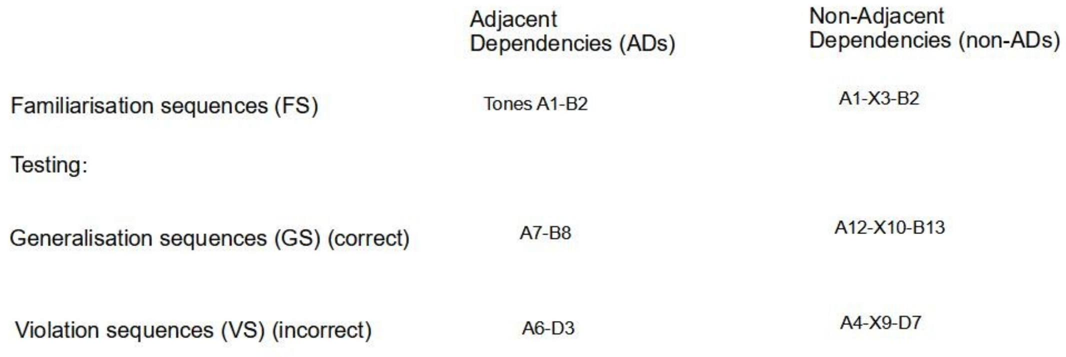
"In language, monitoring syntactic dependencies between words is cognitively demanding yet central to both its acquisition and processing. Unpacking the origins of this computational capacity is therefore key to a holistic understanding of language and its evolution" (Watson et al 2020 p3).

The sentence, "the dog that bit the cat ran away" is an example of a syntactic relationship called "non-adjacent dependencies" (non-ADs) (Watson et al 2020). The phrase "ran away" relates to the dog (which is not adjacent to the action) rather than the cat, while the sentence, "the cat ran away" is an example of "adjacent dependencies" (ADs).

Non-AD processing is important in comprehension of language, and "artificial grammar" experiments have studied it in non-human animals. One such study by Watson et al (2020) compared common marmosets, chimpanzees, and humans using arbitrary computer-generated tones with sixteen pitch-shifted variants. Grammar was taught by the association of "A elements" always followed by "B elements" (AD), for example, or A followed by X than B (non-AD).

The human tests involved instructions to listen to sixty combinations of tones (familiarisation sequences; FS) before testing with new combinations. The 24 participants were instructed to listen for patterns during the FS, and then during testing asked if the sequence followed the rules identified ("Yes" or "No").

The sixteen adult marmosets and seventeen adult chimpanzees were tested by the time spent looking toward the speaker that played the terms (known as a "passive response paradigm"). More time spent looking was taken as the animal noticing an unexpected change (ie: a violation) (figure 13.2).



	Adjacent Dependencies (ADs)	Non-Adjacent Dependencies (non-ADs)
Familiarisation sequences (FS)	Tones A1-B2	A1-X3-B2
Testing:		
Generalisation sequences (GS) (correct)	A7-B8	A12-X10-B13
Violation sequences (VS) (incorrect)	A6-D3	A4-X9-D7

(Based figure 1 Watson et al 2020)

Figure 13.2 - Visual representation of stimuli used by Watson et al (2020).

All three groups of participants detected the VS in testing, suggesting that they had learned the grammar rules (both AD and non-AD) from the FS. At the group level, the chimpanzee and marmosets spent around twice as long looking at the speaker after VS than FS or GS. "There was a large amount of individual variation in each species, with some marmosets giving relatively weak reactions to all sequence types and some chimpanzees not reacting at all (4 of 17 individuals). Human performance was also subject to individual differences, with 20% of participants failing to perform at above chance level" (Watson et al 2020 p3).

The use of different tones in the testing to the FS meant that this "ultimately minimised the likelihood that, during the test phase, individuals simply reacted to deviations from individually memorized sequences, rather than processing the dependent relationships between first and last sound categories" (Watson et al 2020 p4).

Another strength of this study, Watson et al (2020) pointed out, was "a standardised paradigm using identical stimuli, grammars, protocol, and response measures that is nevertheless flexible enough to be applied across species, thus ensuring that any similarities we identified between apes and monkeys in their behavioural responses were likely to reflect shared cognitive mechanisms for processing Non-ADs" (p5).

The main weakness was the use of an artificial grammar (ie: no association between a tone and an object - the semantic aspect of language).

Watson et al (2020) concluded that their findings "indicate that non-adjacent dependency processing, a crucial cognitive facilitator of language, is an ancestral trait that evolved at least ~40 million years before language itself" (p1).

13.5. PRO-SOCIALITY

Pro-sociality is "a voluntary behaviour that benefits others" (Jensen et al 2014 quoted in Dale et al 2019).

This has been tested by giving an animal in a pair the choice of a food reward for themselves only (the "selfish" option; 1/0) or a reward for themselves and their partner (the "pro-social" option; 1/1). Variations include a reward for their partner but not themselves (the "giving" option; 0/1) or no reward for either party (0/0). The control condition has no partner or an inanimate object. This method has been called the "pro-social choice test"; PCT) (Colman et al 1969).

PCT has been used with domestic dogs. Querval-Chaumette et al (2015), for example, used a bar-pull apparatus with two possibilities. The dogs pulled the "giving" option (0/1) more often with a familiar partner than a stranger.

Dale et al (2016) used a method where dogs pressed one of two options on a touch screen with their noses. With a familiar partner, 0/1 was chosen more often than 0/0, as compared to a stranger. Wolves tested also showed pro-social behaviour (Dale et al unpublished data in Dale et al 2019).

Working with rats, Hernandez-Lallement et al (2015) used a maze with two arms - one arm resulted in the "pro-social" option (1/1), and the other in the "selfish" option (1/0). Hernandez-Lallement et al (2015) noted individual differences in the rats' behaviour, though overall 55% of tests ended in the 1/1 choice. Consequently, each rat was given a "social bias" (SB) score, and high scorers were classed as more pro-social.

Dale et al (2019) adapted this method to use with eight domestic dogs and six wolves. The "actor" could see their "partner" in a middle cage, and then decided to enter one of two other cages - actor only reward (OR) (1/0) or both rewarded (BR) (1/1). Training of the animals was performed before testing, and there was also a control condition where no rewards were given after the choice.

Overall, BR choices were not significantly more than OR choices. One wolf, however, showed a high SB.

Dale et al (2019) argued that "methodology plays a crucial role in whether pro-sociality will be observed in a species or not" (p84). House et al (2014), for example, found that chimpanzees were pro-social with one method, but not another. Experimental set-ups are also different to real-life situations (eg: meerkats known to share food, but did not do so in an experiment) (Dale et al 2019).

Dale et al's (2019) methodology was different to Hernandez-Lallement et al (2015), particularly in the amount of training. The failure to show pro-social behaviour by the dogs and wolves was more a problem of understanding than pro-sociality, as other studies have shown the behaviour in these species (Dale et al 2019).

13.6. "STRANGE"

The individual animals studied may not be fully representative of their populations. For example, sampling protocols to trap animals may catch the boldest (Biro and Dingemanse 2009).

Webster and Rutz (2020) proposed the acronym "STRANGE" to understand the representativeness of individual animals studied:

S: Social background - eg: social status; social interactions; opportunities for social learning. One upshot is that how the animals are housed (ie: alone or in groups of different sizes) is important. For example, both canaries and pheasants tested individually in different experiments showed differences in behaviour depending on the size of the group where they were housed during the period of testing (Webster and Rutz 2020).

T: Trappability and self-selection - Selection bias in sampling with individual differences in who gets caught, or the easier to access individuals in large groups or colonies. Webster and Rutz (2020) recommended the use of multiple means to catch individuals.

R: Rearing history - The level of stimulation of the physical environment in which the animals are kept or reared.

A: Acclimatisation and habituation - The changes in behaviour in animals after handling or tagging, or exposure to new testing situations. Domesticated individuals behave differently to feral ones caught.

N: Natural changes in responsiveness - When the research takes place in relation to the animal's life stage, or daily, reproductive or seasonal cycles. For example, honeybees learn better in the morning (Webster and Rutz 2020).

G: Genetic make-up - Laboratory-bred animals are often genetically different to wild ones, and this can lead to "marked differences in behaviour" (Webster and Rutz 2020 p339).

E: Experience - Animals used in multiple experiments learn from previous ones and this is often overlooked in the later experiments. This is particularly so for long-lived animals. Webster and Rutz (2020) asked for more information about this in published papers.

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14. MISCELLANEOUS LIFE

Complex animals (ie: multi-cellular and hard-bodied) are believed to be evolved in the Cambrian period (known as the "Cambrian explosion") after 540 MYA. But evidence has emerged of internal and external skeletons prior to that (during the Ediacaran period) (Wood 2019).

From the beginning of the evolution of life on this planet, three domains have been distinguished (Barras 2020):

- Archaea - microbes with no nucleus (often found in extreme environments).

- Bacteria - single-celled organisms with no nucleus.

- Eukaryotes - all other life forms (animals, plants, fungi).

This three-domain model has been challenged by the finding of eocytes [50]. These are archaea found in sulphur hot springs, for example, which "seemed to share cellular features with eukaryotes" (eg: carrying genes assumed to be unique to eukaryotes) (Barras 2020 p45).

The upshot is a two-domain tree of life, where bacteria and archaea separate, but later archaea separate again, and one branch becomes eukaryotes (Barras 2020).

The origins of life on earth are over three billion years ago, so establishing what happened is far from easy, and consequently there is great disagreement over the three- and two-domain models (Barras 2020).

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[50] Eg: Williams et al (2020).