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Different Animal Behaviours

Kevin Brewer

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Orsett Psychological Services
PO Box 179
Grays
Essex
RM16 3EW
UK

orsettpsychologicalservices@phonecoop.coop

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Kevin Brewer BSocSc, MSc

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://kmbpsychology.jottit.com and http://psychologywritings.synthasite.com/.

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1. DEER VOCALISATIONS AND PLAYBACK EXPERIMENTS

1.1. DEER VOCALISATIONS

Calls (acoustic signals/vocalisations) (appendix 1A) give listeners information about the caller including their physical condition (quality), dominance rank, and level of energy/fatigue. Both potential mates and competitors of the same sex can extract the information using features like calling rate, call duration, and volume.

If the calls are honest signals of the caller's quality, then they must be costly to produce. For example, in mammals the honesty of the signal of physical quality is based on the morphology of the vocal apparatus.

Calls are generated by two elements (Pitcher et al 2014) [1]:

i) The source - vibration of the vocal folds which determine the frequency of the call. This is sensitive to the level of testosterone in the caller, and so is an honest signal about the physiological state of the caller.

ii) The filter - the length of the vocal tract produces spectral peaks (formants) by dampening or enhancing the frequencies. It is an honest indicator of body size. For example, Taylor et al (2011) played growls to dogs with different formants to represent a small dog or a large dog, and the listeners looked at the appropriate sized model of a dog (appendix 1B).

Fallow deer (Dama dama) (figure 1.1) are an interesting species to study in this area. Males tend only to call during a short breeding season (rut) from late September to early November in the northern hemisphere. The call is a "groan", which is short, low-pitched, and stereotyped (ie: unchanging). It is characterised by a series of pulses, and contains six formants within the first 2.5 kHz. The larynx is

[1] The source-filter theory (Fant 1960).

(Source: de:User:Dominik)

Figure 1.1 - Male fallow deer.

retracted during calling, which elongates the vocal tract and decreases the formant frequency (Pitcher et al 2014).

Groaning is related to mating success, and it encodes information about the size, age, and dominance of the caller. The rate of groaning varies depending on the presence of other males in the vicinity and of oestrous females. But, because the males rarely eat during the rut (losing about a quarter of body weight), the acoustic structure of the groans change (mainly from physical exhaustion) (Pitcher et al 2014).

Pitcher et al (2014) investigated the ability of males to recognise changes in the groans with two playback experiments. During the rut in 2011 at Petworth Park, West Sussex, England, twenty-three males [2] at the lek area [3] were studied. Previously recorded calls were used as the stimuli.

The first set of one-minute sequences of groans varied in the rate of groans - 20 or 50 per minute (and

[2] Each experiment involved sixteen males, but nine individuals were used in both experiments.

[3] A lek is an area where all the males congregate, say, and advertise themselves to the females. It is rare among mammals (Goldman 2014).

one minute of silence as a control). the rate signals the arousal of the caller - ie: a faster rate when another male is present or after copulation. The attentiveness of the listener (ie: orienting towards the playback speaker) was the measure of the male's response. This was done from videos with no sound (ie: blind raters).

Listeners were significantly more attentive to calls than silence, both in speed of becoming attentive (latency) and duration of attentiveness. Importantly, the males became attentive significantly sooner to high-rate than low-rate calls (mean: 6.06 vs 10.38 seconds [4]; $p = 0.02$ [5]), and were attentive for significantly longer (mean: 42.00 vs 26.75 seconds [6]; $p = 0.026$). "Thus, fallow bucks are sensitive to changes in groaning rates and perceive higher rates as more threatening than lower rates" (Pitcher et al 2014 p396) [7].

The second set of playbacks used the groans of "early rut" and "late rut". Males spent significantly longer attending to early-rut groans than late-rut ones (mean: 24.38 vs 12.44 seconds; $p<0.001$), but there was no difference in latency. "This demonstrates that males can perceive fatigue-related changes in groans and react differently to early and late rut groans from the same individual, attending more to early rut groans that are indicative of males in better condition" (Pitcher et al 2014 p396).

Fatigue produces a loss of co-ordination in the vocal production system (eg: hoarse groans), and thus is an honest signal of that. This is a "current-state signal" (Bergman and Sheehan 2013). The ability to perceive information about the caller means that the listener will know whether that individual is vulnerable to challenge (eg: when tired late in the rut period).

1.2. APPENDIX 1A - PRINCIPLES OF COMMUNICATION

Communication requires a signaller and a receiver. The signaller can give an honest signal (accurate information) or a dishonest one (false information) [8]. The receiver takes into account the trustworthiness of the signaller as to whether to respond or not. If the receiver does not respond, the signaller may stop signalling.

This simple relationship can be seen in a signal-

[4] Control = 46.31 seconds.

[5] Wilcoxon signed-ranks test (repeated measures design).

[6] Control = 3.19 seconds.

[7] Charrier et al (2011) found that male Australian sea lions (Neophoca cinerea) responded more aggressively to playbacks of higher rates of barking.

[8] Deception takes many different forms in the animal kingdom (appendix 1C).

response game used by Polnaszek and Stephens (2014) with blue jays (Cyanocitta cristata). A pair of birds were placed in two adjacent cages with a transparent partition. There were two perches in each cage, and one bird (signaller) was taught to choose one to signal to the other bird (receiver) to copy. For example, the signaller chose the left perch, and the receiver copied, and both birds received a reward. This is an honest signal. A light above the perch told the signaller which perch to choose.

The signaller is then given a reward if the receiver chose the wrong perch. This provided an incentive for a dishonest signal. For example, a light appeared above the left perch, the signaller moved to the right perch.

The signaller will stop signalling if the receiver does not respond. The receiver ignored the behaviour of the signaller if it was always dishonest.

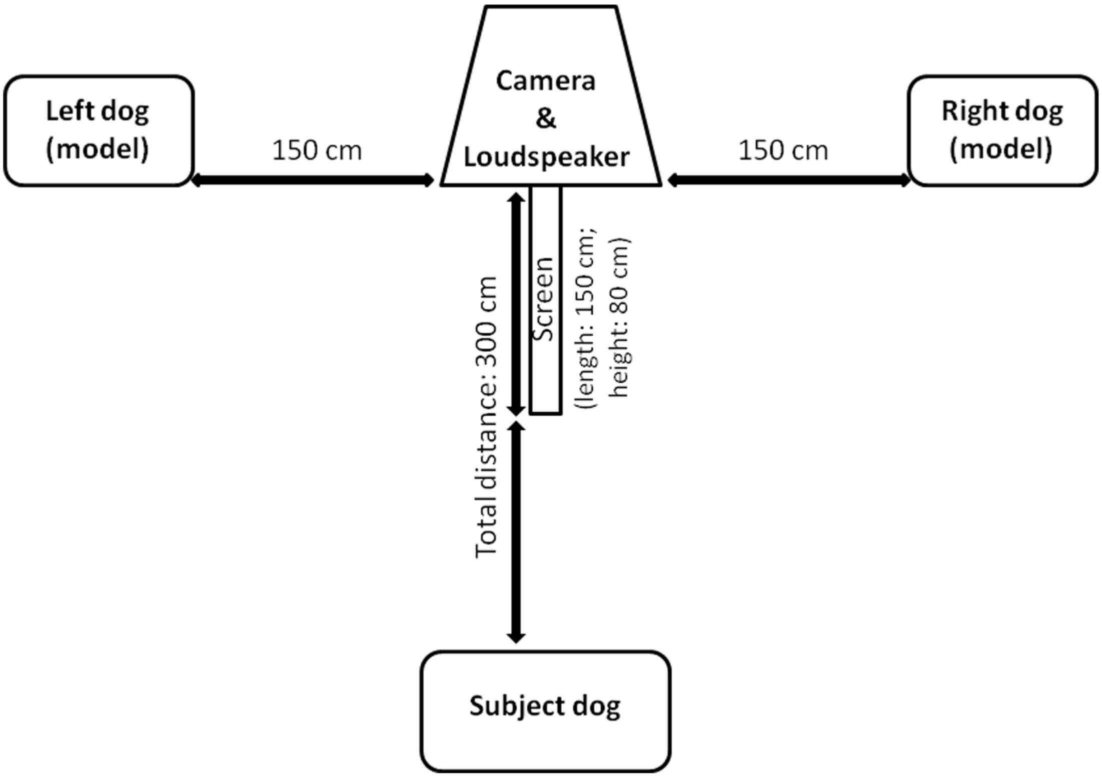
The level of certainty in the environment also influences communication. In a second experiment, Polnaszek and Stephens (2014) showed this by varying the information the receiver had independent of the signaller. In the high certainty condition, a light appeared above the correct perch of the receiver as well as the signaller. So, the receiver could tell if the signaller was being honest, and there was no room for dishonest signals.

When the environment had low certainty (ie: the receiver did not have independent information), the receiver accepted some dishonest signals without stopping responding. This is known as "receiver tolerance for imperfect signal reliability". In low certainty environments, it pays the receiver to heed dishonest signals if the signals are "honest on average". The low certainty environment allowed the signaller greatest exploitation (ie: use of dishonest signals).

1.3. APPENDIX 1B - TAYLOR ET AL (2011)

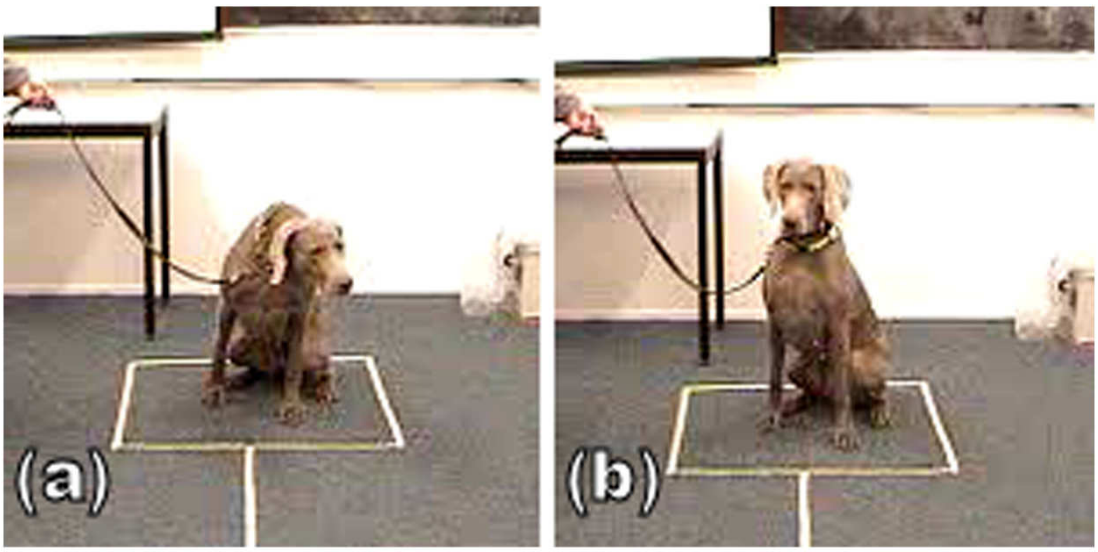
Taylor et al (2011) used a preferential looking paradigm in their experiment. Dogs were presented with two stuffed dog models - a Jack Russell terrier (small dog) and a German shepherd (large dog) as they were played growls from a small and a large dog lasting 25 seconds (figure 1.2). The position of the models and the order of the growls was counterbalanced.

Forty adult dogs, whose owners had volunteered in response to an online advertisement, were used in the study. Testing took place at a dog training centre in southern England. The procedure was filmed, and later, without sound, raters coded the direction of the look and the duration (figure 1.3).



(Source: Taylor et al 2011 figure 2)

Figure 1.2 - Experimental set-up.



(Source: Taylor et al 2011 figure 3)

Figure 1.3 - Dog looking at the left model (a) and the right model (b).

The dogs looked at the correct model (ie: same size as growl) significantly more times than the incorrect one, and for significantly longer time (mean: 7.6 vs 3.7 seconds). The researchers felt that the findings were "unequivocal evidence that domestic dogs have the ability to match size information in the acoustic domain with corresponding size information in the visual domain in an ecologically valid environment" (Taylor et al 2011).

The ability to determine body size from acoustic information is an honest signal (ie: difficult to fake) whereas visual information may not be completely reliable (eg: male elephant seals rear up to appear larger to competitors).

1.4. APPENDIX 1C - SEXUAL DECEPTION

Mating signals produce a strong response in the receiver. Sexual deception is where such signals are used by other species to exploit the receiver [9]. Predators may use sexual deception to get prey, like the bolas spider which mimics the female sex pheromones of moths to lure a male or the katydid that mimics the female part of a cicada mating call duet to bring the male within striking distance (Lehtonen and Whitehead 2014) [10].

The risk of sexual deception should lead to an "evolutionary arms race" [11] where the receiver evolves a way to avoid mimics (eg: mating signal changes) [12]. But this does not always happen because of "the difficulty in minimising the costs of being fooled without incurring the cost of falsely rejecting real mating opportunities" (Lehtonen and Whitehead 2014 p52).

The receiver trades accuracy against error (figure 1.4). As long as the benefits of positive accuracy outweigh the costs of errors, then co-evolution will not occur. For example, a few males are deceived by mimics but the majority find mates.

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[9] Deception generally can be seen in the evolution of mimicry (appendix 1D).

[10] An opposite phenomena to sexual deception is exaggerated honest communication as in the "handicap principle" (Zahavi 1975). Wasteful displays, altruism, and facing danger are signals used by males to communicate their good quality genes via this principle (Hawkes and Bliege Bird 2002). For example, among the bird, Arabian babblers (Turdoides squamiceps), males compete to do sentinel duty, and to distract and fend off predators from the co-operative breeding site, as well as provide food to others (Zahavi 1990). "Displays that supply such benefits are readily noted by other babblers. Demonstration of the capacity to beat the cost of these displays substitutes for overt threats, which potentially lead to fights that could be even more costly for the signaller and at least some of the audience" (Hawkes and Bliege Bird 2002 p59).

[11] Antagonistic co-evolution (asymmetric interspecific arms race) (Dawkins and Krenbs 1979).

[12] Stowe (1988) described it as "increasing signal discrimination on the part of the dupe, and increasing signal refinement on the part of the mimic" (quoted in Lehtonen and Whitehead 2014).

	Receiver Responds	Ignores
Mate - true signal	Positive accurate - mating opportunity	False negative - reject mate
Mimic - false signal	False positive - deceived	Negative accurate - avoid deception

Figure 1.4 - Options for receivers.

1.5. APPENDIX 1D - MIMICRY

Mimicry is where one species evolved to resemble another in some way. It is usually an edible species evolving to look like an unpalatable/toxic one (ie: as defence against predators). This is Batesian mimicry (or "'parasitic' charade"). But mimics can also deceive their own prey ("aggressive mimicry") (Nelson 2014).

Mimicry can occur for different senses, including (Nelson 2014):

1. Vision - Jumping spiders known as Myrmarachne have evolved to resemble aggressive ants as well as copying their movements.

2. Sound - A palatable species of tiger moth mimics acoustic signals of a noxious species to fool echolocating bats.

3. Chemical - Certain butterfly species mimic the chemical signals of ants in order to deposit eggs in the ant's nest for protection.

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2. FIVE BEHAVIOURS RELATED TO MATING

2.1. SEXUAL PARASITISM

Sexual parasitism is where a tiny male permanently attaches himself to a much larger female. It is seen in some deep-sea ceratioid anglerfish, where, at the extreme, females are sixty times longer than males and half a million times heavier (Pietsch 2005).

Anglerfish live in low density populations in the darkness of the deep ocean (eg: daytime depth of >300 m; Pietsch 2005) so there is a high risk of not finding a mate. Males have evolved into "little more than parasitic testes" (Cooke et al 2008) that are permanently attached to the female. In some cases, "attachment is followed by fusion of tissues and apparently by a connection of the circulatory systems so that the male becomes permanently dependent on the female for blood-transported nutrients, while the host female becomes a kind of self-fertilising hermaphrodite" (Pietsch 2005).

Pietsch (2005) distinguished three reproductive modes:

i) Obligatory parasitism - Males "apparently never mature unless they are in parasitic association with a female, and, likewise, females never become gravid until stimulated by the permanent parasitic attachment of a male" (Pietsch 2005 p232).

ii) Facultative parasitism - Males "probably attach to females whenever the two meet regardless of sexual readiness. If both partners are in a state of readiness at the time of attachment, spawning and fertilisation take place, after which the male releases his hold on the female and is then presumably capable of beginning a new search for another mate. If one or both partners are not ready to spawn, the male remains attached until spawning can take place. The longer the male remains attached to the female, the greater are his chances of becoming fused and establishing a permanent parasitic association" (Pietsch 2005 p230).

iii) Temporary non-parasitic attachment - Male and female tissue not fused.

2.2. HYPERAGGRESSIVE MALES

Behavioural syndromes (or "animal personalities") is a term that covers the consistency of an individual showing a particular behaviour across multiple contexts, and the difference between individuals on a particular behaviour. Behaviours studied in different species include activity, boldness, aggressiveness, tendency to explore, and sociability (Sih et al 2014).

Individual differences have a relationship to mating success as, for example, more active and exploring males encounter more females or more aggressive males win more fights with other males over females. But the context is also important. For instance, bold, aggressive individuals do better in low-risk environments (ie: against shy, non-aggressive individuals) than in high-risk environments (ie: against other bold and aggressive individuals) (eg: risk of injury from fights). There has to be a mix of types in a social group (Sih et al 2014).

For example, hyperaggressive males, who attempt to forcibly mate with males, females, pairs, juveniles, or even other similar species, are disruptive to a social group by sending both males and females into hiding or away, and thereby reducing mating activity (and success) generally. Such individuals are classed as "keystone individuals" (appendix 2A) (Sih and Watters 2005) because they have "a disproportionately large effect on the overall group's social dynamics and thus on individual and group outcomes" (Sih et al 2014 p10).

Hyperaggression can be viewed as a poor social skill or social competence (ie: maladaptive behaviour for the social group).

Sih et al (2014) investigated this behaviour experimentally with the insect, the stream water strider (Aquarius remigis) (figure 2.1). Individual males collected in Stebbins Cold canyon, California, USA, were rated for activity and aggressiveness [13], and then the mixture of types in a social group was manipulated. Six males and six females were used in each group, and the level of aggression of the males was varied as high, medium or low.

Males with a higher active-aggression score had more mating activity (ie: proportion of time mating), but

[13] Scored from 0 to 3: "0 = males showed little or no movement and did not initiate interactions; 1 = males were active, touched other individuals and occasionally performed jumps; 2 = males were active and jumped most individuals encountered, but only struggled with females; 3 = males actively followed other individuals and had extended struggles with most individuals (females, males or pairs) encountered" (Sih et al 2014 p12).

(Source: Megodenas)

Figure 2.1 - Water strider.

hyperaggression led to lower mating activity. The mating success of all males in the group was reduced by the presence of hyperaggressive individuals, but more active-aggressive individuals (who were not hyperaggressive) fared better than low active-aggression individuals.

Hyperaggressive males should be selected against. Why do they exist? Sih et al (2014) offered three possible answers:

a) They are the maladaptive extreme of the distribution of aggression (ie: pathological).

b) Hyperaggressiveness is beneficial in certain circumstances - where females are difficult to find, or where there are few competing males who can be kept away from the females.

c) Indirect social selection - "Social selection on behaviour is the product of the social selection gradient (the effect of the group's trait on the individual's mating success) and the covariance between the individual's trait and the social group's trait. Here, the social selection gradient, the effect of hyperaggressive males on male mating success is negative, and intriguingly, the covariance between the individual and the group's trait is also negative. That is, by being hyperaggressive, a male substantially reduces the chance that another male in his group will become hyperaggressive, thus obviating the cost of living with a hyperaggressive male" (Sih et al 2014 p16).

2.3. FRESH FACES AND THE RARE-MALE EFFECT

Where females prefer uncommon or unfamiliar males of the species, the "rare-male effect" will occur. This is where males who have a rare or novel characteristic have greater mating success than the "common" males. This is seen in the Trinidad guppy (Poecilia reticulata) (figure 2.2), for example [14].

(Source: User:Jdiemer)

Figure 2.2 - Male guppy.

Females of this fish species prefer males with unfamiliar or rare colour patterns, and females change their preference based on prior exposure to patterns (ie:

[14] This behaviour has also been reported among insects, lizards, and other fish (Graber et al 2015).

less exposure). Females can be said to engage in negative-frequency-dependent mating (NFDM) (Graber et al 2015).

This behaviour could be explained by the idea of a "fresh face" (Hughes et al 2013) (ie: choosing the next male who is different to the previous male encountered). Graber et al (2015) tested this idea in the laboratory, and also investigated which aspects of appearance the females pay attention to (novel colour patterns or amount of orange body colour).

Graber et al (2015) allowed a virgin female guppy to interact with four males (of which there were two pairs where males were similar to each other in colour patterns but different to the other pair). The sexual response of the female (ie: a C-shaped posture) to the male's courtship display was used as the measure of preference (by two independent observers).

In total, 861 courtship bouts were observed. The females were twice as likely to respond to a male who was different to the previous male to court her during a 30-minute observation period. But this behaviour did not occur 24 hours later with the same fish. The researchers were not sure why the behaviour changed over 24 hours. Possibly the females came to distinguish between the similar males, or "physiological changes unrelated to learning that occurred in the 24 hours after virgin females first mated could account for the change in preference" (Graber et al 2015).

Males performed more courtship displays towards females when the performer was different to the previous male. Independent of colour pattern, females preferred males with more orange body colouration.

This study showed NFDM or the "fresh face" preference in short time periods. Males tend to move around larger areas while female guppies are more stationary. A preference for the "fresh face" would favour arrivals, and avoid inbreeding (In Brief 2014).

2.4. POST-MATING SELF-CASTRATION

Male coin spiders chew off their heavy genitals (emasculation) after their one lifetime mating, and this makes them more able to mate guard. This "extreme monogamy" is risky for the males (ie: one-shot with one female), and so mate guarding is important (In Brief 2015).

Kunter et al (2015) found that self-castrated males (ie: eunuchs) stayed closer to females and attacked rival males more aggressively than virgin males.

Emasculation occurs in a few spider and fly species, and at three points - pre-maturation, mating, and post-mating. Spiders have two sperm transferring organs (palps), and emasculation can produce half or full eunuchs, as well as variation in the degree of damage (eg: breakage of genital tip vs both palps) (Kuntner et al 2015).

Different theories have been proposed to explain emasculation in spiders, including (Kuntner et al 2015):

i) Plugging hypothesis - Broken male genital parts during mating are left in the female copulatory organ. Thus securing a genital plug which stops the sperm of rival males.

ii) Better-fighter hypothesis - Eunuchs have no future reproductive possibility and so are more aggressive towards other males while mate guarding. This could explain post-mating emasculation.

iii) Gloves-off hypothesis - The removal of heavy palps allows the male to have superior fighting abilities in pre-mating fights. This could explain pre-maturation emasculation. It could also give the male more endurance in mate guarding.

iv) Remote-copulation hypothesis - Detached genitals during copulation allows continued sperm transfer after mating.

Kuntner et al (2015) tested these hypotheses in relation to post-mating emasculation in the South and South-East Asian coin spider (Herennia multipuncta). With sixty males, nine became half eunuchs and 23 full eunuchs, while the remainder did not mate. This suggested that post-mating emasculation is obligate in this species.

1. Testing plugging hypothesis - After mating where there was a broken palp as a plug, 23 females were offered the opportunity to mate with another male. In no cases was the second mating possible.

2. Testing better-fighter hypothesis - Male fights were observed between twenty-six post-mated eunuchs and rivals on the web of the females and points were assigned for level of aggression. The control condition involved a pair of virgin males on the web of a virgin female (n = 19 contests). Eunuchs were significantly more aggressive and remained significantly closer to the female than virgin males.

3. Testing gloves-off hypothesis - The endurance of the males was measured as time until exhaustion in response to gentle paintbrush touches by the experimenters. Eunuchs had significantly longer endurance than virgin males.

The experiments found support for all three hypotheses in explaining post-mating emasculation in this coin spider - ie: the broken genitals plug the female (plugging hypothesis), and the male effectively mate guards (better-fighter and gloves-off hypothesis). "Emasculation seems to be a male strategy intended to reduce or avoid sperm competition with their rival males and thereby secure their paternity share. This behaviour may only be in the male interest or in the interest of both sexes if the eunuch behaviour conserves female energy that would otherwise be wasted on deterring unwanted copulations" (Kuntner et al 2015 p125).

2.5. LEK SIZE

Leks are where groups of males gather to sexually display to visiting females. For a female "it affords her the opportunity to make more reliable, simultaneous comparisons of available mates and it reduces her expenditure of time and energy in travel during mate seeking and evaluation... [while]... males may prefer to display at leks because the aggregation sites are specific locations that allow more effective transmission of signals and attraction of many females" (Alem et al 2015 p106). Leks may also give the benefits of "safety in numbers" in relation to predators for both males and females.

But a lek does not include all the males in a population. What determines the size of a lek? For males it is the costs of group living like increased aggression or risk of disease transmission, while females may find it difficult to identify the best males in a massive lek, for example, or face too much male harassment (table 2.1). These are classed as "economic" costs, but perceptual constraints may also limit the lek size (Alem et al 2015).

Alem et al (2015) explored the ideal lek size in five experiments with the lesser wax moth (Achroia grisella) (figure 2.3) [15]. The males gather together and produce ultrasonic songs [16] to attract females in the vicinity (up to 1 m away).

[15] These moths infest honeybee colonies. The samples came from Tours, France, and Kansas, USA, but were kept in a laboratory in France.

[16] The song is made by fanning the wings which causes a pair of tymbals at the forewing base to buckle and emit a pair of short pulses with a time gap between them (known as the asynchrony interval). Males can sing for 6-10 hours each night. Females prefer songs with faster pulse rhythm, at higher amplitude, and with a longer asynchrony interval (Alem et al 2015).

<table>
<tr><th>Advantages</th><th>Disadvantages</th></tr>
<tr><td>Males:
• Greater per capita mating success.
• Group defence against predators.
• Lone males risk being missed by females.
• Effective transmission of signals (eg: longer distances).

Females:
• Less time and energy than searching for dispersed lone males.
• Easy comparison of males available.
• Group defence.</td><td>Males:
• Increased aggression, and general stress.
• Risk of disease transmission.
• Groups attract predators.
• If too large, expensive to compete with other males.

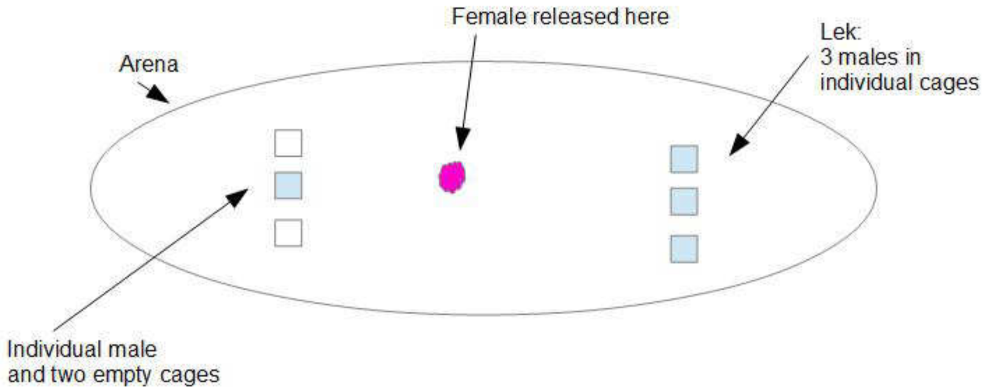
Females:
• Too many males = problem in decision who is best.
• Time and energy to travel long distance to lek.
• Male harassment risk.
• Risk of sensory overload.
• Increased stress etc of groups.</td></tr>
</table>

Table 2.1 - Advantages and disadvantages of lekking for males and females.

(Source: Sarefo)

Figure 2.3 - Lesser wax moth (mounted in museum).

The first experiment offered a female a choice of a lone singing male or a group at different ends of a small arena (figure 2.4). The group varied between two and five males, and the female had three minutes after release to make a choice (ie: move to within 2 cm of the male(s) for at least ten seconds). There were four conditions (1 vs 2, 1 vs 3, 1 vs 4, 1 vs 5), and twenty females were used in each condition. Significantly more females choose the group than the lone male (over 70%).



(Based on Alem et al 2015 figure 1a p109)

Figure 2.4 - Example of Experiment 1 set-up.

Experiment 2 varied the choices: 4 vs 2, 5 vs 3, 6 vs 4, 7 vs 5, 8 vs 6, and 9 vs 7 males (along with 1 vs 3 as control). Significantly more females choose the larger group of males for the 4 vs 2 and 6 vs 4 conditions, but for the other options there was no significant difference in the female choices.

Is it just the number of males that influence female decisions of where to go? Experiment 3 compared the song of a lone male and males in a group of three, and found that the song in a group had an accelerated rhythm by about 15%. Experiment 4 then tested whether the female could distinguish the difference. Using playback of the songs from the previous experiment, twenty-two females showed no preference.

The final experiment tested whether a male preferred to be with other singing males. This was similar to Experiment 1 but a male had the choice of a lone singer or a group, instead of a female. The male moved towards the other singers (as opposed to staying separate) but with no preference.

Overall, a female preferred male leks of up to 4-6 members, while a male joined any other singers. Thus "no evidence suggesting that larger male groups repelled additional males from arriving and joining them" (Alem et al 2015 p113). The most effective lek size in terms of per capita attractiveness [17] was three.

[17] This is number of females that chose lek divided by number of males in lek.

2.6. APPENDIX 2A - KEYSTONE INDIVIDUALS

Keystone individuals include high-ranked alpha individuals, conflict mediators, facilitators of group cohesion, bridge individuals that aid information flow between social groups ("keystone nodes" - highly connected individuals), superspreaders (of disease), and "bad apples" (eg: cheaters) (vs "golden fruit") (Sih et al 2014). Other terms used include elites, dominants, organisers, leaders, and pioneers or population founders. "Although these words have subtly different definitions or connotations, the feature that they share in common is that they all describe individuals with an inordinately large influence on surrounding conspecifics" (Modlmeier et al 2014 p54).

The importance of these individuals to the group can be seen in experiments where they are removed (or added), for example:

- Insect - among one species of ant (Formica schaufussi), an individual organises large prey retrieval, and removal of this "organiser" led to the prey being abandoned (Robson and Traniello 2002).

- Fish - among zebrafish (Danio rerio), removal of the key fish reduces the performance on a group-foraging learning task (Vital and Martins 2011).

- Mammal - adding a hyperaggressive male to a group of yellow baboons (Papio cynocephalus) had negative effects on the group leading to a violent shift in dominance hierarchies including stressed females and increased spontaneous abortions (Alberts et al 1992).

Removal of the keystone individual has serious consequences for group dynamics, whereas removal of an individual in a keystone role is less important as they are soon replaced. "The reason for this would be that a keystone individual has a more pervasive, individually unique influence that cannot be replaced by a mere generic individual" (Modlmeier et al 2014). An example of a keystone role is an "elite" worker Temnothorax ant during nest relocation, who, when removed, is replaced by another worker (Pinter-Wollman et al 2012).

Keystone individuals can be fixed (ie: influential for a long period as in alpha males) or episodic (for a limited period, like a "organiser" of a scouting trip by ants) (Modlmeier et al 2014).

Modlmeier et al (2014) offered three possible explanations for keystone individuals:

i) Keystone-conferring genotypes - The individual has inherited a characteristic that is beneficial to the group, and that other individuals do not have. Thus this characteristic remains in the population in evolutionary terms. It is less clear for negative keystone individuals who are detrimental to the group, unless enforced change and instability caused by hyperaggressive males, for example, has benefits to the group.

ii) Early experiences - eg: the individual at the top of a feeding dominance hierarchy, as in rainbow trout. So, "an experienced individual may sometimes monopolise a limited resource and enjoy an augmented growth rate and body condition which, in turn, allows that individual to maintain persistent control over said resources" (Modlmeier et al 2014).

iii) Hormones - eg: juvenile level of testosterone and future dominance in baboons.

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3. SOCIAL LEARNING IN THE WILD: KNOWN BUT NOT SEEN

3.1. CHIMPANZEES

A novel behaviour within a group can occur through individual or social learning. Individual learning is where each individual learns the behaviour themselves through trial and error, say, and it is coincidence, to some degree, that many individuals in that group had learned the behaviour. Social learning involves one individual learning the behaviour, and then others learn from that individual by imitation, for instance [18].

Social learning has been reported among groups of chimpanzees that have been extensively studied, like the Sonso chimpanzee community of the Budongo Forest, Uganda [19]. This community has been continuously observed for around twenty years with individual animals known individually [20].

Social learning of novel behaviour among captive chimpanzees is undisputed (Hobaiter et al 2014). But "to date, there have been no direct demonstrations of novel behaviour spreading socially within a wild chimpanzee group" (Hobaiter et al 2014).

Hobaiter et al (2014) reported the first observation of two novel behaviours in the Sonso community in November 2011 [21] - "moss-sponging" and "leaf-sponge re-use". Moss-sponging is the use of moss as a sponge to collect water to drink [22], while leaf-sponge re-use is "utilising a previously fabricated and used sponge that had been discarded on a previous visit, in contrast to standard leaf-sponging where an individual collects

[18] Social learning is a more sophisticated version of simple observational learning (appendix 3A), and there are many examples of learning in the animal kingdom (appendix 3B).
[19] This is a semi-deciduous forest area in the western Rift Valley.
[20] Animal behaviour can be altered by the presence of observers and researchers (appendix 3C).
[21] Sixty-eight named individuals known to the researchers at that time.
[22] "Moss-sponge, following Lanjouw (2002), is defined as follows: 'chimpanzees collected moss off the bark of the trees, loosely rolled it into a bundle, generally not bigger than a few centimetres wide'. Moss-sponge was inserted into the mouth at least once before sponging. In both previous cases, the sponges appeared exclusively composed of moss despite leaves being freely available" (Hobaiter et al 2014).

leaves from a branch" (Hobaiter et al 2014).

The moss-sponge was first seen used by an alpha male ("NK"), and then in the next six days by six other members of the group. The researchers felt that the spread of the behaviour was too swift to be individual learning. They used a statistical technique called network based diffusion analysis (NBDA), which "tests whether or not a novel behaviour spreads along a social network, as would be expected if social transmission were involved" (Hobaiter et al 2014).

de Waal stated that this study was "the first on apes to show by means of networking analysis that habits travel along paths of close relationships" (quoted in Brahic 2014).

However, Hobaiter et al (2014) admitted that "our results do not allow us to identify the precise learning mechanism employed during the social transmission of moss-sponging, it remains possible that this may vary from those on which humans rely to transmit their culture".

3.2. APPENDIX 3A - SIMPLE OBSERVATIONAL LEARNING TO SURVIVE

"Sexual conflict, the evolutionary divergence in the interests of males and females..., can drive the evolution of certain traits favourable for one sex but costly to the other" (Scardamaglia et al 2015 p9). Sexual cannibalism is one such conflict (table 3.1).

Females	Males
Feeding and thus increased reproductive output. But too early interrupts sperm transfer.	Prolonged sperm transfer and thus more eggs fertilised. But only if future mating opportunities scarce.

Table 3.1 - Evolution of females eating males after copulation.

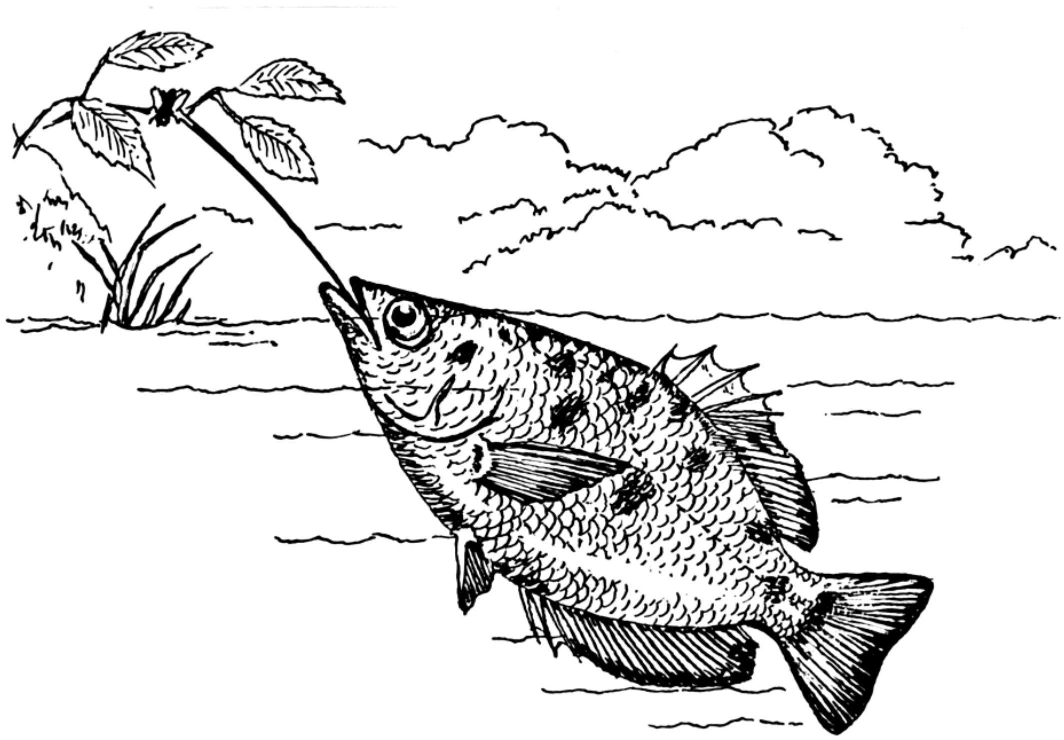
Ultimately, males pay the cost of death, and this has produced behaviours to reduce cannibalism - eg: "death feigning" by nursery web spider (Pisaura mirabilis), or waiting for female to feed before courtship initiation (black-legged nephila spider; Nephilia fenestrata) (Scardamaglia et al 2015). Also observation of the female's body as well-fed females are less likely to consume mates (Scott 2015).

Among praying mantids, where about one-third of mates are cannibalised, males try to elude detection by the female by a slow approach and from the rear, or mating when the female is feeding (Scardamaglia et al 2015). Also males arrive together and can observe the behaviour of females towards other males.

Scardamaglia et al (2015) showed this in a study of a praying mantid (Parastagmatoptera tessellata) in Argentina. A male was offered the choice of an aggressive and a non-aggressive female after seeing how the two females behaved towards another male. The observer males preferred the non-aggressive females every time.

3.3. APPENDIX 3B - BALLISTIC HUNTING TECHNIQUE

The archerfish (Toxotes jaculatrix) is able to fire jets of water (eg: diameter of 3 mm from 15-60 m) to dislodge stationary prey on branches above the water (figure 3.1). Their accuracy with a single shot is high, and the prey vary from flies to small lizards.



(Source: Pearson Scott Foresman; in public domain)

Figure 3.1 - Drawing of archerfish shooting.

Schlegel et al (2006) found that the fish fine-tune the strength of the shot to prey size (as the shot is costly in energy terms) (ie: the shot is about ten times the forces that the prey could maximally sustain).

Once the fish has fired its shot, it cannot be corrected, so the shooter needs to account beforehand for the distance of the target, and the optical distortion of looking from water into air. Also they must be able to predict where the prey will fall into the water.

Schuster et al (2006) tested archerfish on moving targets. Training was given for the horizontal movement of the target at three different heights above the water. The fish that learned to hit the moving target appeared to have accounted for the movement before firing rather than broadening the water jet's diameter or firing multiple shots.

The researchers also discovered that the fish used observational learning. Four fish were allowed to watch another fish learning to hit the moving target. "The initial performance of four of the four observers almost approached that of their long-trained model, and most importantly, was in each case clearly far above the score the practicing model was able to reach when it had started its practice. Thus, the observer fish must have been able to learn the task from extensively watching the performance of their practicing group member" (Schuster et al 2006 p382). Archerfish live in schools, so observational learning may not be that surprising (as compared to solitary animals).

3.4. APPENDIX 3C - HUMAN-ANIMAL INTERACTIONS

Long-term observation of animals requires them to become habituated to the repeated and non-threatening presence of humans. But human observers have an influence on the animals in, say, their predator-prey interactions. For example, Stanford (1998) reported that chimpanzees in Gombe National Park, Tanzania, being followed by human observers used the fear that the presence of humans induced in red colobus monkeys to "flush" out this prey.

Isbell and Young (1993) found less leopard predation of vervet monkeys being observed in Amboseli National Park, Kenya, than when the observers were not present in the area. This situation has been called the "human shield effect" (Berger 2007).

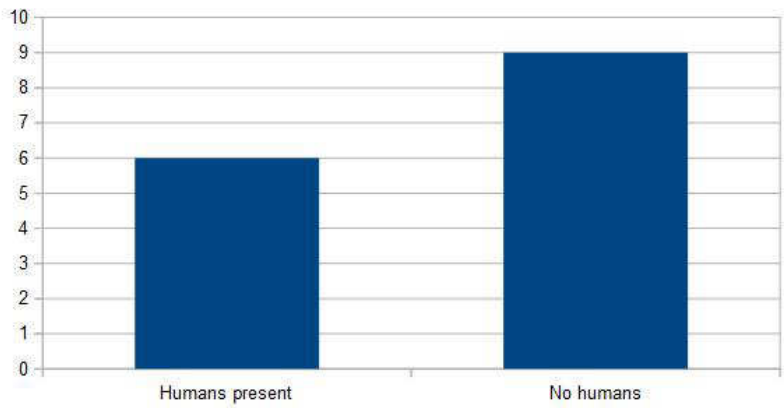
The "human shield effect" is a "reduction in vigilance that prey animals exhibit when human observers are present" (Goldman 2014). It is a specific version of the "observer effect" - ie: individuals change their behaviour when they know they are being observed.

But how to quantify this effect? One technique is called the "giving-up density" (GUD). This is the amount of food left behind in an experimental food patch (ie: food left out to encourage animals to come to be observed). Animals that feel safe and perceive less risk of predators will eat more food, and thus there is a lower GUD.

Nowak et al (2014) used this method with two groups of samango monkeys (Cercopithecus mitis erythrarcus) being observed in a forest area of the Soutpansberg Mountains, South Africa. These monkeys generally perceive a greater risk the lower down their forage. So their GUD is greater for food on the ground than in the tree tops (ie: a negative correlation between GUD and height above ground of food).

The researchers left a standard amount of food (25 shelled peanuts) at four different heights (0.1, 2.5, 5.0, and 7.5 m above ground) each day. Forty days of observational data were used (ie: 20 days x two groups of monkeys). On nineteen of these days, observers were following the monkeys, and on the other days there were no humans present. Camera traps were used in the latter condition. The food was left out at 7 am, and the remainder was measured (GUD) at 4 pm each day.

When humans were present, the GUDs were significantly lower at all four heights than with no humans, but especially at the ground level (0.1 m) (figure 3.2). The monkeys perceived less risk when observers were present, and humans were seen as shields particularly against terrestrial predators.



(Based on Nowak et al 2014 figure 2a and 2b p1203)

Figure 3.2 - Average number of peanuts remaining (GUD) (out of 25) at ground level based on presence of human observers or not.

Humans can be perceived as predators by prey even though they do not attack the prey. Prey will respond with anti-predator behaviour like fleeing. The distance to the predator when the prey flees is known as the flight initiation distance (FID), and it is used as a measure of the prey's risk assessment. A greater perceived risk produces a larger FID [23]. The reduction in FID can be used as a sign of habituation (ie: lowering in perceived risk) to humans who do not predate the animal.

McGowan et al (2014) studied this with blue-tailed skinks (Emoia impar) (figure 3.3) on Mo'orea [24], French Polynesia [25]. Humans do not predate these animals, but come into contact in daily interactions.

(Source: Chris Brown USGS; in public domain)

Figure 3.3 - Blue-tailed skink.

The first experiment tested whether skinks become habituated to humans. A researcher approached a skink in a standardised way [26] while an observer estimated the FID. This was done in four different areas of Mo'orea where human presence varies. In total, there were 87 experimental approaches. The FID was significantly lower at the site where humans were regularly present (around a

[23] "Risk assessment is a costly behaviour..., especially if prey repeatedly respond to false threats. Habituation allows prey to reduce energy expenditures and focus their time on fitness-enhancing activities" (McGowan et al 2014 p1087).

[24] North of Tahiti.

[25] Also known as Society Islands.

[26] When a skink was sighted, the approacher moved to the starting distance (2-6 m away), waits five seconds, and then directly approaches silently at 0.5 m per second while maintaining eye contact. An observer records the FID by marking in some way the skink's position and the approacher's position when flight occurred.

small dump) (145 cm) than a pristine area inaccessible by vehicles (191 cm).

The second experiment tested whether the skinks responded differently based on the number of humans approaching. Skinks were approached by one human alone, one human who had been standing with two others, or three humans. There were eighty experimental approaches used in the analysis. The FID was greater for three humans approaching than the other two conditions (figure 3.4).

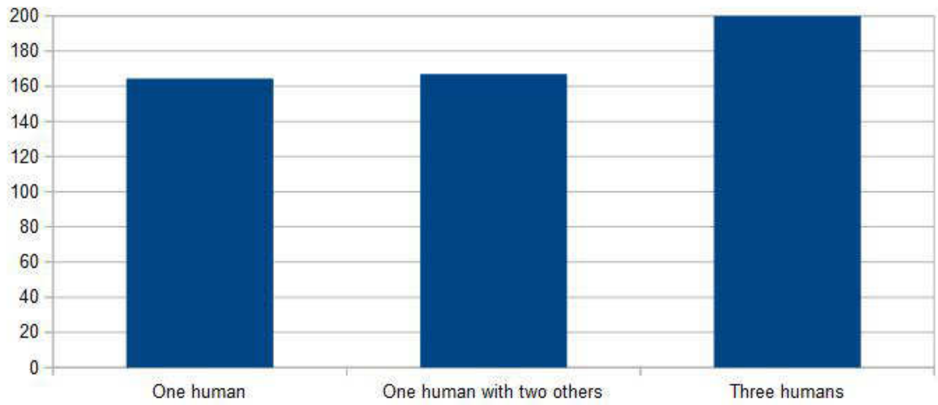


Figure 3.4 - Mean FID (cm).

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4. INSECT MIGRATION

Stefanescu et al (2013) began: "Large parts of the world are characterised by the seasonal abundance of resources, interspersed by periods when resources are unavailable or when the physical environment is inhospitable for survival. Species can exploit such resources in situ by means of diapausing [27] or other arrested stages... or, alternatively, by some form of migration, breeding when temporary resources become available and then retreating to locations where survival is possible at other times of the year" (p475) [28].

The term "animal migration" [29] usually brings to mind movements to-and-fro (eg: to a warmer climate and back to breeding area), most commonly by birds. This flapping-wing flight migration also occurs in some insects, like butterflies and moths, locusts, and dragonflies (appendix 4A). However, insects migrate using other means (Reynolds et al 2014).

1. Non-flapping-wing flight (airborne migration).

Wingless terrestrial arthropods use air currents (anemohoria) to move either with silken lines ("ballooning") or not. There are preparatory behaviours for "lift-off" which suggest the movement is intentional. For example, spiders climb high up, assume a "tip-toe" posture, facing into the wind, and release a silk thread until the wind drags on it and lifts the spider away (Reynolds et al 2014).

"Ballooning" has been reported in some species of spiders and spider mites, and the larvae of some moths (Bell et al 2005). The latter use "suspended ballooning", where they lower themselves from a leaf, say, on a silk line and wait for the air current to take them away (Reynolds et al 2014).

Windborne migration without silk is used by some mites, for example, which move to the edge of a leaf and allow their body to be lifted off by air currents. Experiments have shown that this behaviour is intentional. For instance, mites will choose not to become airborne if the smell of a prey is present on the current leaf, but will move if no smell is there

[27] A state of dormancy or delayed development.

[28] The monarch butterfly (Danaus plexippus) combines both - southwards migration in North America to Mexico to enter diapause over the winter (Stefanescu et al 2013).

[29] The key aspect of migration is the intentional movement away from the present habitat or "home range" (ie: a "temporary suppression of station-keeping responses" (Reynolds et al 2014) and often feeding ("appetite response"). Migration differs from "ranging" (Dingle 1996), which involves movement further afield often when there is a shortage of resources. Put another way, ranging is an expanded foraging behaviour (Reynolds et al 2014).

(Reynolds et al 2014).

2. Pedestrian migration

This includes running (cursorial movement), walking (ambulation), hopping/jumping (saltation), and limbless crawling. Examples of this type of migration include the mass movements of New World army ants, Eciton burchelli and Eciton hamatum, and the "march" of some locust species (Reynolds et al 2014).

3. Waterborne migration

The use of water currents (amenohydrochoria) to produce the movement, often by insects in larval stages that dwell in rivers and streams. There is also "rafting" of floating on the water surface by terrestrial arthropods (Reynolds et al 2014).

4. Wind-propelled migration on the surface of water ("sailing" or "skimming") (eg: aster root aphid; Pemphigus trechernei) (Reynolds et al 2014).

5. Phoresy

This "entails one organism 'hitchhiking' on the body of another (usually larger and more mobile) organism" (Reynolds et al 2014 p20) (eg: mites; pseudoscorpions attach to appendage of a fly or beetle species) (Reynolds et al 2014).

APPENDIX 4A - MULTI-GENERATION MIGRATION

Migration may occur because of reproductive benefits - ie: more offspring, and surviving, in new than current habitat. But in the case of insects with short lifespans, an individual migrates northwards to breed in the spring and summer, say, and it is their offspring than return southwards for the winter (as compared to birds where the same individuals go and return).

For example, the silver Y moth (Autographa gamma) migrate north in the spring about 300 km per night using fast-moving airstreams 200-1000 m above ground, from North Africa and the Middle East to Northern Europe as they struggle to survive the summer at southern latitudes. Then a southward migration in the autumn as they cannot survive the winter in northern latitudes. This moth breeds continuously with at least five generations per year (Chapman et al 2012).

Chapman et al (2012) used data from one hundred light traps, and entomological radars to map the migrations into and out of the UK of the silver Y moth between 2000 and 2009 (10-240 m individuals into UK each spring). Greater numbers moved south out of the UK in autumn than had arrived in the spring suggesting that the population had increased (2-4 times). It was estimated that the migration produced a larger overall population, even accounting for death during the movement, than if the moths had not migrated. Thus a reproductive benefit to multi-generational migration.

Stefanescu et al (2013) described the migration of the painted lady butterfly (Vanessa cardui) between Africa and Europe involving six generations in a complete cycle [30]. A northwards movement from Africa to Europe in the spring, and the reversal in late summer and autumn. "Exodus from each region takes place before the environment becomes directly inhospitable, in anticipation of the arrival of conditions unsuitable for continued breeding in the location of adult emergence. Adverse seasonal conditions not only include extreme temperatures and the decreasing availability of ephemeral resources for larvae and adults, but also increasing levels of natural enemies such as specialist parasitoids..." (Stefanescu et al 2013 p483).

The researchers used thousands of everyday observations as part of "citizen science programmes", and systematic butterfly monitoring schemes as well as insect-monitoring radar in 2009.

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[30] There may be as many as eight generations in a year with the larval stage lasting 30-60 days and then as an adult for 10-24 days (Stefanescu et al 2013).

5. ANIMAL SLEEP

5.1. INTRODUCTION

The study of sleep in humans has distinguished three elements (Randler 2014):

i) Sleep duration - amount of time asleep.

ii) Sleep fragmentation or sleep quality - eg: number of awakenings during sleep or the depth of sleep.

iii) Sleep timing (or chronotype) - when the sleep occurs during the 24-hour cycle. Humans show a preference of sleeping earlier at night to sleeping later.

Steinmeyer et al (2010), for example, found individual preferences for timing of sleep among free-living blue tits (Cyanistes caeruleus) based on video recordings of nestboxes for sleep onset, awakening time, and latency to sleep (ie: time taken to fall asleep). If chronotype has a genetic basis, which it is argued for humans, than it is not surprising to find individual differences in other species (Randler 2014).

Another parallel with humans is in adolescent sleep changes. At the onset of puberty (eg: 12-14 years old) there is a change to evening orientation (or eveningness) (ie: sleeping later), and a return to morningness at the end of puberty. This pattern has been observed in rhesus monkeys, and laboratory mice and rats (Randler 2014).

Sleep-wake patterns are affected by natural environmental factors like temperature and light, and the artificial environment (eg: urban factors). In the former case, great tits became active (ie: woke) and stopped (ie: sleep) earlier at higher than lower temperatures (Randler 2014). While male songbirds living near streetlights started their dawn chorus significantly earlier than in a forest (Randler 2014).

5.2. MUCUS COCOONS

Some coral reef fishes (eg: wrasses and parrotfishes) produce a mucus cocoon [31] from specialised

[31] Mucus cocoons are produced by other fish in different situations (eg: aestivation) (appendix 5A).

glands in the gill cavity in which they sleep at night. This may protect against predators (eg: Winn and Bardach 1959) or bacteria (eg: Videler et al 1999).

Winn and Bardach (1959) reported that spotted moray eels (Gymnothorax moringa) ate more of three species of parrotfish that did not produce cocoons than of a species that did. Grutter et al (2011) criticised this study as many individuals of the cocoon-producing species were eaten in the experiment.

Grutter et al (2011) showed that the cocoon acted like a "mosquito net" and protected against parasites that feed on the blood of the fish. Thirty-eight bullethead parrotfish (Chlorurus sordidus) (figure 5.1.), collected from the Great Barrier Reef, Australia, were placed in individual tanks. Half had their cocoons removed when asleep. Gnathiids (parasites) were placed in each tank for four and a half hours. Significantly more fish without a cocoon were attacked by the parasites than with cocoons (94.4% vs 10% of fish).

(Source: Jaroslaw Barski http://rafy.pl/galeria.php?sel=Z2FsZXJpYS9iYXJza2ky)

Figure 5.1 - Bullethead parrotfish.

5.3. APPENDIX 5A - AESTIVATION AND MUCUS COCOON

Aestivation [32] is "a state of torpor at high temperature" (Chew and Hiong 2014). For example, African lungfishes (Protopterus annectens) enter aestivation during food shortages using a dried mucus cocoon. This allows them to survive in air or underground when water has evaporated during the dry season.

Aestivation has three phases in lungfishes (Chew and Hiong 2014):

1. Induction - environmental cues produce physiological changes including the secretion of mucus, which becomes the dried mucus cocoon in 6-8 days.

2. Maintenance - completely encased in the cocoon, feeding and movement cease. This lasts for over six months [33].

3. Arousal - stimulation by water, for example.

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[32] This is the opposite of hibernation in cold temperatures. Hibernation is possible because the participants do not experience physiological problems that humans would face in the same situation. For example (Nordrum 2015):

- Blood flow to the brain (and consequently oxygen) is drastically reduced without any permanent brain damage (eg: arctic ground squirrels 90% drop).
- Reduced heartbeat produces lactic acid when sugars broken down (ie: anaerobic rather than aerobic metabolisation), which can be damaging if it builds up (eg: arctic ground squirrels break down fats instead of sugars for energy).
- Preparation for hibernation requires the intake of large amounts of food without any negative health effects (eg: grizzly bears gain 100 lbs in short period).

[33] A case of seven years has been reported (Hiong et al 2013).

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