

## **6. FORAGING**

### **6.1. DECIDING TO STAY OR GO**

Food tends to have a heterogeneous distribution. This means that it is not necessarily available regularly - ie: spatially clumped (distribution across an area) or temporally clumped (only available at certain times). Animals can respond to this situation by the use of foraging strategies, which are based on search or ambush (ie: sit and wait) (Higginson and Ruxton 2015)<sup>32</sup>.

The search strategy has been addressed by optimal foraging theory<sup>33</sup> (Stephens and Krebs 1986), which attempts to predict when an animal will move to a new food patch. The ambush strategy requires a decision of where to sit and for how long (ie: risk of starvation). Choosing a location frequented by regular prey is important.

Animals can use either or both of these foraging strategies. Each strategy has costs as well as - for example, searching uses energy and risks encountering predators. The combination of costs and benefits is known as the "currency" of the strategy (Higginson and Ruxton 2015).

The switching of strategies is influenced by prey abundance (eg: ambush during very high abundance)<sup>34</sup>. Higginson and Ruxton (2015) made some observations about the strategy used:

a) When searching and waiting use similar energy (eg: gliding birds), animals will use search more as availability of food increases, or food is less concentrated in clumps, or food is more ephemeral (ie: only available for a limited time period).

b) When the predator cost of searching is high (ie: greater than energy cost) (eg: well-camouflaged animals), increased food density should lead to less intensive searching (ie: more waiting), but when energy cost is greater than predator cost (eg: well-defended animals), the opposite will happen. Well-camouflaged individuals will search only if food is scarce (ie: benefits of finding food compensate for greater predator risk). Well-defended individuals (with, say, chemical defences) will use a search strategy as food becomes abundant.

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<sup>32</sup> The ability to return home after foraging (ie: homing) is important (appendix 6A).

<sup>33</sup> It is "based on the concept of natural selection as a fitness-maximising algorithm, where fitness is assumed to depend on the dominant costs and benefits associated with behavioural options" (Higginson and Ruxton 2015 p122).

<sup>34</sup> Switching strategy is similar to reward downshift studied in the laboratory (appendix 6B).

c) Risk of starvation and fat reserves are important factors <sup>35</sup>. When fat reserves are low, searching is better compared to ambush when fat reserves are high.

Assuming that animals can switch between foraging strategies, then the choice of strategy will be influenced by costs of searching, risk of starvation (if wait), and prey distribution (Higginson and Ruxton 2015).

Animals, however, stay longer at a food patch than theory would predict because the cost of moving is key in the decision to stay (conservative strategy) or go (riskier strategy). This decision is also influenced by the behaviour of others in social foragers, like the caterpillar of the forest tent caterpillar moth (*Malacosoma disstria*). Individuals follow the pheromone trails of the first caterpillar that begins moving. But this "does not lead to optimal foraging, as groups can become trapped by pheromone trails on the first food source contacted, even if it is nutritionally inadequate... While the nutritional costs of being trapped on a poor food source are obvious, a conservative foraging strategy might be adaptive if the exploration costs of leaving a known food source are greater than the potential benefits of discovering a superior alternative" (Santana et al 2015 p246). Older caterpillars, though, are more independent.

Santana et al (2015) designed four experiments to test the foraging decision-making of these caterpillars.

Experiment 1 - To test food preference when choices nearby (ie: two host leaves placed next to each other). Food preference was defined as "at least 75% total consumption on a single leaf". Younger (second-instar <sup>36</sup>) groups of caterpillars made a choice, while older caterpillars (fourth-instar) were less selective.

Experiment 2 - Two different leaves were offered but with a distance of 20 cm between them. The groups of caterpillars were left on one leaf to see if they would move to the second leaf. The younger caterpillars tended not to move while the older ones did.

Experiment 3 - To test the effect of group size on decision to stay or go among younger caterpillars. This experiment was the same as the previous one, but either groups of 10, 40 or 100 individuals were left on one leaf. Group size did not affect the tendency to stay, and

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<sup>35</sup> For example, low body mass triggers longer foraging trips in little penguins (*Eudyptula minor*) (Reynolds et al 2015).

<sup>36</sup> Instar = moult.

the groups consumed the whole leaf before moving.

Santana et al (2015) summed up the first three experiments: "Second-instar caterpillars usually remained on the known food source, irrespective of host species or of group size, suggesting that, at this stage, exploration costs outweigh the benefits of selective feeding. Larger groups could draw particular advantages from consuming a known food source completely before searching out a new one. In the field, large groups of second-instar *M. disstria* caterpillars can fully consume a leaf within days..., and resource depletion can be severe, especially during outbreaks when many colonies exploit a single tree. In this situation, excess choosiness would likely be disadvantageous. Thus, although larger groups can travel faster over unmarked ground than smaller groups..., they also benefit from consuming all the food available rather than risk searching for a better alternative" (p248).

Experiment 4 - To test if younger caterpillars would leave a least preferred food source when a pheromone trail was present or not. When a trail was present, caterpillars moved in 83% of trials compared to 8% of trials without a trail.

Santana et al (2015) stated: "Experiment 4 suggests that costs associated with exploring unknown territory (ie: moving off a pheromone trail into unexplored territory) play a key role in driving the low likelihood of patch leaving. When younger caterpillars were presented with trails away from a less preferred food source, effectively eliminating unknown territory costs, groups were more likely to leave the first food source and discover a novel one. These unknown territory costs include the risk of not finding another food source, the risk of losing purchase on the smooth bark surface and falling out of the tree..., and the risk of being separated from the group" (p248).

Overall, these caterpillars showed a conservative foraging strategy because the costs of moving from the current patch are greater than the benefits of finding a new food source.

## **6.2. PRODUCER OR SCROUNGER**

Another foraging strategy relates to finding own food or joining another individual who has already found food - eg: as in ground-feeding birds. The former is a "producer" and the latter is a "scrounger" (Afshar et al 2015). In a group of animals, too many scroungers is detrimental, but a small number is not a problem. How is a balance achieved?

The key seems to be the predictability of food. Afshar et al (2015) presented zebra finches (*Taeniopygia guttata*) with seeds each day that varied in amount or not. One bird was released to find food in different feeders ("patches") in the cage, and the behaviour of the following birds were scored as producer (search for own food) or scrounger (join first bird). Overall, "the birds gradually increased their level of scrounging over time in the variable treatment and decreased it over time in the non-variable treatment" (Afshar et al 2015 p184).

This was taken as evidence of "risk-sensitive foraging behaviour" as "producing was a more uncertain foraging strategy than scrounging because producers rely on their own effort and have a more variable payoff than scroungers... Scrounging, therefore, is thought to be a variance-averse strategy... because scroungers can exploit the effort of several individuals and are thus less sensitive to changes in patch quality variance than they are to the average patch richness... Scrounging more under increased patch variance may therefore offer a stable solution to a less certain environment..." (Afshar et al 2015 p184).

Speed of learning is also important, as fast learning individuals respond more quickly to changes in the environment. Fast learning individuals can switch strategy (ie: producer or scrounger) quicker (Afshar et al 2015).

### **6.3. ROLE OF PARASITES**

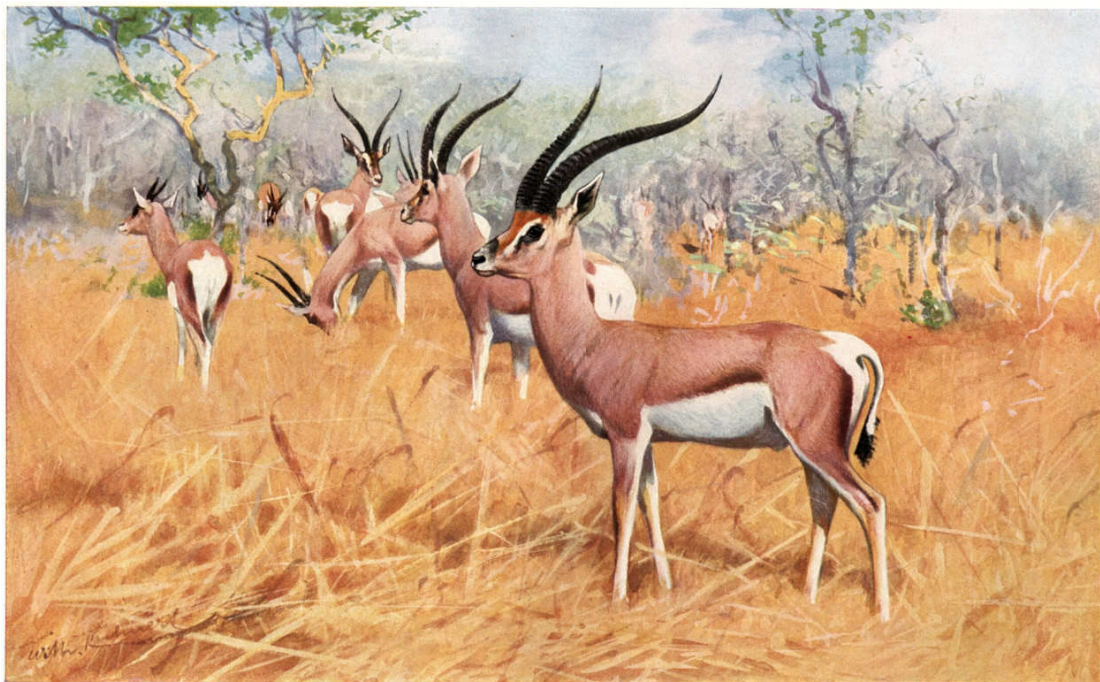
Individuals vary in the amount of time spent on different activities, and the parasite load has an affect. For example, in an experiment by Fenner and Bull (2008) that reduced the parasites in an Australian lizard (gidgee skink), individuals spent significantly more time basking in the sun than controls.

It has been suggested that gastrointestinal nematode infection produces "feeding depression" (ie: reduced foraging) (Worsley-Tonks and Ezenwa 2015).

Worsley-Tonks and Ezenwa (2015) manipulated the parasite (nematode) load in female Grant's gazelle (*Nanger granti*) (figure 6.1) in Kenya with an anthelmintic drug for 120 days. Long-distance observations of the animals categorised their behaviour over twelve hours per day into foraging, vigilance, resting, moving, or other. Treated animals spent significantly more time foraging than controls (40% vs 28% of time observed). Worsley-Tonks and Ezenwa (2015) summed up: "Although we cannot rule out other ecological and environmental factors as potential causes of the difference in foraging

behaviour observed between treated and control females during the treatment period, this effect is consistent with previous studies on domestic ruminants showing that nematode infection can induce reductions in forage intake" (p51).

The treated group also spent less time in vigilance. Worsley-Tonks and Ezenwa (2015) explained this finding thus: "...treated females were in better condition and thus better able to escape predators. These 'good condition' females may therefore have the flexibility to invest less time in costly anti-predator activities with no negative consequences" (p52).



(Source: Brehms Tierleben, Small Edition 1927; in public domain)

Figure 6.1 - Drawing of Grant's gazelles.

#### 6.4. NEOPHOBIA

During the exploration of their environment animals will come across novel objects. The willingness to approach such objects is described as neophobia-neophilia, with highly neophobic animals being slow to do so, while highly neophilic animals are quick to approach novel objects (Moretti et al 2015). Stowe et al (2006a) defined neophobia as "the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past" (quoted in Moretti et al 2015). "Neophobic responses can therefore reduce exposure to danger but they can also constrain

explorative behaviour and thus opportunities for learning and innovating" (Moretti et al 2015 p159).

Neophobia can also vary with the presence of conspecifics. It is reduced in some cases (eg: gerbils eat novel food after seeing another gerbil eat it), and increased in others (eg: great tits) (Moretti et al 2015). While, for example, individual ravens approach a novel object faster when alone (than in pairs), but spend more time close to it and manipulating it when with other ravens. Also ravens approach the object faster when with siblings than non-kin, while dominant males approach first if paired with a female but not with a male (Stowe et al 2006b).

Moretti et al (2015) showed differences in neophobia in eleven hand-reared wolves and twelve dogs in Austria. The thirty-eight novel objects used in the experiment included a bicycle, a book, balloons, and a teddy bear. In a repeated measures design, all animals were tested alone, in pairs with different pack members, and with the whole pack. During the video-recorded fifteen-minute trials, behaviours were scored, like willingness to approach the object (eg: sniff it), how quickly the object was first approached (ie: move to within one metre) (approach latency) and to touch for the first time, and total time investigating the object.

In around 10% of trials, dogs did not approach the object whereas the wolves always did. This was a significant difference. But there was no difference in approach latency.

Both species manipulated the object for less time alone than in the other conditions <sup>37</sup>, but wolves manipulated the object more than dogs generally.

Moretti et al (2015) explained the differences between wolves and dogs as "domestication effects: wolves jumped back more often, made contact with the object more slowly and investigated the objects for longer than dogs. These results indicate a greater interest of wolves in novelty, but also greater neophobia than dogs. Hence, the fact that all wolves but not all dogs approached the novel objects, even though wolves showed more fearful reactions than dogs, seems to be an indication of less interest by the dogs rather than neophobia" (p166).

## **6.5. EFFECTS OF EARLY STRESS**

The experience of stress at a younger age has later

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<sup>37</sup> Moretti et al (2015) noted: "as predicted, we found significant facilitation effects for the manipulation of objects in the pair and pack conditions as compared to animals tested alone. This suggests that risk sharing may be an important form of co-operation in both wolves and dogs" (p166).

consequences for animals, both in terms of physiology and behaviour. For example, wood frogs exposed to early predator threat had large limbs and narrower bodies as adults, while young laboratory rats who encounter a cat explore new environments less as adults (Chaby et al 2015).

Even in the womb, there is an effect: "maternal stress during gestation, or shortly thereafter, can cause phenotype adjustments in offspring that are adaptive if the maternal environment predicts the offspring environment" (Chaby et al 2015 p42). For example, European starlings exposed to stress in the egg, hatch smaller and thus need less food. This would fit with a challenging environment (ie: less food available) (Love et al 2005).

Focusing on stress during adolescence in laboratory rats (ie: when the hypothalamic-pituitary-adrenal axis, which controls the body's stress reaction, is maturing), studies find conflicting results. On the negative side, there is memory impairment, but enhanced decision-making on the positive side in adulthood (Chaby et al 2015).

The thrifty phenotype hypothesis (Hales and Barker 1992) and the maternal mismatch hypothesis (Sheriff and Love 2013) proposed that "early exposure to an adverse environment will prepare individuals for a high-threat environment, but may detract from performance under low-threat conditions" (Chaby et al 2015 p38).

Chaby et al (2015) found support for this idea in their experiment with twenty-four male Sprague-Dawley laboratory rats <sup>38</sup> in the USA.

Half of the rats received stress each week between 30 to 70 days old (ie: adolescence) in the form of small cage, crowding, and fox urine, for example (table 6.1) (adolescent-stressed group; AS). The unstressed control group had none of these experiences.

Then at around 110-140 days old the rats were tested for foraging performance in a low- and a high-threat condition (figure 6.2). The latter included bright light, which rats do not like, and hawk vocalisation and visual cue (ie: silhouette), whereas the low-threat condition was dim light only. A Plexiglas arena was used which included seven objects (eg: plastic sand toys), and each object contained "Cheerios" (which the rats were familiar with) (a total of fifteen were available in each trial). The amount of food eaten, how quickly the individual moved towards the food, and movement between patches of food were the measures of foraging performance used.

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<sup>38</sup> An albino rat specially bred over the years for laboratory research. Originally one male and six females by Sprague-Dawley company in 1925. Currently "owned" and bred by Harlan Laboratories ([http://www.harlan.com/products\\_and\\_services/research\\_models\\_and\\_services/research\\_models/sprague\\_dawley\\_outbred\\_rat.hl](http://www.harlan.com/products_and_services/research_models_and_services/research_models/sprague_dawley_outbred_rat.hl); accessed 11/08/14).

STRESSOR	ADOLESCENT-STRESSED GROUP	CONTROL GROUP
Physical: Small cage Damp bedding Cage tilt	25% smaller 200 ml of water 30° angle	Standard size Dry bedding No tilt
Social: Isolation Crowding Foreign bedding	Left in clean cage Two rats in cage Bedding of other rat	No isolation No crowding Always own bedding
Predation: Bobcat model Fox urine Cat fur Feline vocalisations	Near cage Sprayed in cage Placed in cage Sounds of 5 cats	Not used No smell Not done Silence

Table 6.1 - Details of stressors.

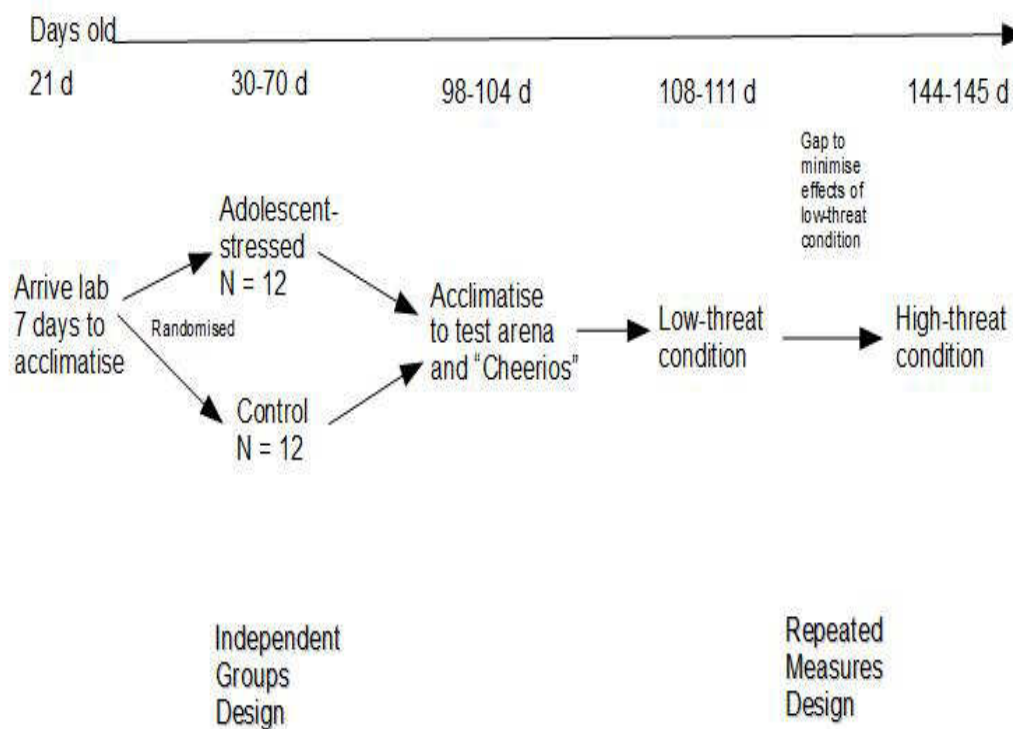


Figure 6.2 - Overview of procedure of Chaby et al (2015).

In the low-threat condition, AS rats took longer to begin foraging than controls (mean: 3.5 vs 1.7 secs), though the same total amount of food was consumed between groups. But in the high-threat condition, the AS rats began foraging quicker (mean: 5.1 vs 5.6 secs), moved



between food patches more (around 20%), and consumed more food than controls (mean: 8 vs 6 "Cheerios"). Chaby et al (2015) calculated that AS rats would be full in 4.12 hours, but the control rats would take 5.88 hours to obtain daily nutrient requirements.

The AS rats showed "apparent increased resilience" in the high-threat condition. Chaby et al (2015) offered three possible explanations for the findings:

i) The AS rats adjusted more easily to the high arousal of the high-threat condition because of their earlier experiences.

ii) The AS rats always behaved as if threat was high, which is adaptive in a high-threat environment, but maladaptive when low-threat.

In a natural environment, Orrock and Fletcher (2014) (appendix 6C) found that wild mice acted as if predators were present in an area that once had many predators in the past (eg: 24-28 rat generations ago).

iii) The AS rats compared the current threat to their past experiences and "interpreted the high-threat cues as less threatening".

## **APPENDIX 6A - HOMING**

Dell'Aricecia et al (2015) investigated Mediterranean storm petrels' (*Hydrobates pelagicus melitensis*) ability to return to the same nest each year after winter migration. Birds nesting in artificial nestboxes in two caves on Isle de Benidorm, Spain, were studied.

In the first experiment, prior to the birds' arrival in March 2012, nestboxes were moved. Ten nestboxes were moved a short distance (eg: 25 cm), and ten a longer distance (eg: 250 cm) (with nineteen untouched as controls). The birds did not return to the displaced nestboxes (only 4-15%) compared to the controls (93-100%).

In the second experiment, a Y-shaped maze was designed which offered the birds a choice of nests. The birds showed no clear choice based on smell. Of 38 birds who made a choice out of fifty-three tested, sixteen chose their own nest and twenty-two the other nest.

The results of both experiments showed that the Mediterranean storm petrels did not use odour recognition for homing to their nest in the long-term (ie: after migration) or short-term (ie: after foraging), but that nest position was key in the former case.

Dell'Aricecia et al (2015) explained their findings thus: "In Benidorm, during the 2 years of our experiment,

we observed average partner fidelity of only 76.8%... As a consequence, the use of the partner's odour to recognise the nest would require the learning of different partners' odours and the cognitive capability to frequently update the target odour. The use of the partner's odour to recognise the nest might be a costly strategy, and not the most efficient one for nest discrimination. Mediterranean storm petrels may, therefore, disregard olfactory information in favour of more constant and reliable cues. For instance, the topographical features of the cave remain constant in space and time and they could serve as landmarks to relocate the nest crevice" (p103).

## **APPENDIX 6B - REWARD DOWNSHIFT**

The basic principles of learning and reinforcement see rewarded behaviour as continuing. So if every time a lever is pressed, for example, a food pellet is received, the behaviour of pressing the lever will continue. It is learned. There is also an expectation of reward. What happens if the reward is reduced (ie: a "downshift in reward magnitude")?

Thorndike (1911), who outlined the basics of stimulus-response learning with the "law of effect", argued that there would be a gradual decline in the behaviour if the reward was reduced. An alternative is known as "successive negative contrast" (SNC) (Flaherty 1996). The immediate response to a downshift in reward is an exaggerated decline in the behaviour.

Reward downshift is not just stopping the reward, but it also relates to the quality of reward (eg: favoured food to less favoured food). For example, Davies et al (2015) measured hens' speed to reach a food reward when less preferred food was given after getting used to a preferred food. For six trials it was the preferred food, then a shift on trial 7, and the less preferred food was given for trials 8 to 14. The speed to reach the food (latency) on trials 8 to 14 was key. Becoming significantly slower than a control group who received the less preferred food on all fourteen trials would support SNC, whereas a gradual slowing is what Thorndike predicted. The data gave support to the latter. "Hens that experienced a downshift in food reward took longer to reach the food than before the shift, but their post-shift latency did not differ from that of control birds that had experienced the less preferred food throughout" (Davies et al 2015 p26).

## APPENDIX 6C - ORROCK AND FLETCHER (2014)

Orrock and Fletcher (2014) showed that anti-predator behaviour continues after the prey is gone and later returns, suggesting that "prey in natural settings are cognisant of the dynamic nature of their predators over timescales that span many years".

The researchers studied the anti-predator behaviour of deer mice (*Peromyscus maniculatus*) (figure 6.3) in response to the island fox (*Urocyon littoralis*) on San Miguel Island (part of Californian Channel Islands; figure 6.4) over six years after return of the predator. The foxes had declined in population and the remaining were removed to a captive breeding programme, later to be re-introduced.



(Source: Centers for Disease Control and Prevention; in public domain)

Figure 6.3 - Deer mouse.

Foraging trays were left around the island in different sites (eg: exposed or sheltered). The mice forage at night, and clear moonlit nights are considered risky because the mice can be detected more easily. On these nights, foraging was less (especially in sheltered sites<sup>39</sup>), irrelevant of fox numbers. But on nights with rain or low moonlight (ie: safe foraging nights), mice

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<sup>39</sup> Foxes are better than flying predators at attacking mice in shrubs, for example.



(Source: Lencer)

Figure 6.4 - Location of San Miguel Island.

reduced their foraging in exposed areas as fox numbers increased.

The island had virtually no foxes for the equivalent of 24-28 mouse generations, yet the prey did not lose their anti-predator behaviour (ie: the relaxed selection pressure did not produce an evolutionary loss of anti-predator behaviour).

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## **7. BIOLUMINESCENCE IN THE OCEAN**

Bioluminescence is "biologically produced light that is detected and acted upon by organisms" (Rivers and Morin 2012 p2680) <sup>40</sup>.

Blue is the most common colour (which travels farthest through seawater) followed by green, while violet, yellow, orange, and red are rare (Widder 2010).

Light can be produced in three ways (Rivers and Morin 2012):

i) Intracellular ("intrinsic luminescence"; Haddock et al 2010) - chemical reaction within cells in the body called photocytes) (Widder 2010).

ii) From bacterial symbionts

iii) Extracellular - eg: cypridinid ostracods use a chemical reaction that includes oxygen in sea water (ie: chemicals released directly into the water) <sup>41</sup>.

Judson (2015) pointed out that four-fifths of bioluminescent organisms live in the ocean <sup>42</sup>, and listed the main groups - ostracods ("tiny animals that look like sesame seeds with legs") (figure 7.1), dinoflagellates ("speck-of-dust size beings named for their two whip-like flagella and the whirling motion they make"), light-making fish (eg: myxophids, hatchetfish) <sup>43</sup>, squid, shrimp, ctenophore, worms, sea cucumbers, siphonophores ("sinister, string-like predators with long, stinging tentacles that hang down like a curtain"), radiolarians (amoeboid beings), and bacteria.

Bioluminescence can be used in three main ways <sup>44</sup>:

1. As defence by prey.

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<sup>40</sup> Bioluminescence is distinct from fluorescence (where molecules technically do not produce their own light) and phosphorescence (more common in minerals) (Haddock et al 2010).

<sup>41</sup> Oxidation of a light-emitting molecule (luciferin) with a catalyst enzyme (luciferase or photoprotein) (Haddock et al 2010).

<sup>42</sup> Many organisms using bioluminescence are in the deep ocean (below 1000 m) where there is no visible light (Widder 2010).

<sup>43</sup> At least 42 families across eleven orders of bony fishes (Haddock et al 2010) - eg: flashlight fish (*Photoblepharon steinitzi*) use bioluminescence to see and attract prey, to confuse and avoid predators, in courtship, and to form groups (Rivers and Morin 2012).

<sup>44</sup> Haddock et al (2010) noted: "Bioluminescence serves many functions for marine organisms, and it frequently serves multiple roles for a single organism. One of the caveats in interpreting the ecological roles of bioluminescence is that types of light emission seen during laboratory stimulation may not reflect how they appear in nature, any more than one would conclude that human vocalisation is an anti-predatory response because we cry out when poked" (p463).





(Source: Davidjhorne)

Figure 7.1 - Images of ostracods via microscopes.

i) Surprise - a bright flash that startles a predator and the prey escapes (eg: squid).

ii) Smoke screen - glowing fluid or cloud of sparks that misdirects the predator allowing the prey to escape (eg: shrimp, vampire squid).

iii) Decoy - the prey jettisons glowing body part (eg: deep-sea squid *Octopoteuthis deletron*). This may also be a "sacrificial tag", where lost tissue continues to glow after removal from body, even for hours in the predator's stomach (and draw attention of their predator) (Haddock et al 2010).

iv) Camouflage - eg: shining underbelly that matches the light from the surface and conceals the prey from predators below. This is counter-illumination, used by fishes (eg: midshipman fish), crustaceans, and squid that inhabit twilight depths and have predators with upward-looking eyes (Widder 2010).

Cookie-cutter shark (*Isistius brasiliensis*) combines counter-illumination and prey attraction. A dark band below the mouth looks like the silhouette of prey of larger fish, say, who approach and the shark takes a bite

out of the body of the animal (Widder 1998).

v) "Burglar alarm" - light that makes the predator visible and alerts the predator's predator, or mark the predator with luminescent slime (Widder 2010).  
Dinoflagellates (prey) use against mysid shrimp (predator) to attract midshipman fish (predator's predator - secondary predator) (Mensinger and Case 1992).

Campagna et al (2001) found that southern elephant seals used the "burglar alarm" of some species to help in "lighting the way" to find the desired prey.

vi) Warning (aposematism) - eg: to signal prey as toxic (eg: scale worms).

## 2. During attack by predator.

i) Shock - a flash of light that stuns the prey (eg: squid).

ii) Lure - the prey is drawn to a glowing lure (eg: anglerfishes).

iii) Beacon - predators use the prey's bioluminescence to know where the prey is gathering.

iv) Searchlight - to locate prey.

## 3. Reproduction/courtship - to signal ready to mate (eg: pelagic octopods, ponyfishes).

Rivers and Morin (2012) compared the bioluminescence of *Photeros annecohenae* (found in the Caribbean sea) in courtship and defence displays. In the former, short pulses of light are produced, while in defence the ostracod "releases copious quantities of luminescence that appears as bright, enveloping, swirling clouds of light, which coincides with the pumping frequency of the fish's gills" (Rivers and Morin 2012 p2863). Not surprisingly, defence displays have a much greater energy cost (estimated at 25% of the maximum luminescent potential of the individual compared to 5% for a courtship display). Put another way, a male would have to display "on average, 50 times to equal the luminescent output of a single, average defensive display, and 200 times to equal that of the maximum observed defensive display" (Rivers and Morin 2012 p2865).



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## **8. NATAL DISPERSAL AND THE EXPLODED LEK SYSTEM**

### **8.1. DISPERSAL**

Many juveniles (on the edge of breeding maturity) leave their family/birth habitat and move elsewhere. This is natal dispersal <sup>45</sup>. It reduces the risk of inbreeding <sup>46</sup>, and the problem of competition over resources with kin, for example, but it is costly in terms of finding an appropriate habitat (Hardouin et al 2015). There may be sex differences in dispersal in some species (Greenwood 1980).

Hardouin et al (2015) used the opportunity of the release in Morocco of seventy-nine captive-bred North African houbara bustards (*Chlamydotis undulata*) (figure 8.1) in the wild over eight years (2001-9) to study the sex differences in dispersal. The birds had radio-collars to aid the researchers in following them. The net dispersal distance (NDD) was measured. This is the distance between the release site and where the bird settles (eg: to display).

Males had a larger NDD than females (mean 27 vs 13 km). Males released with close kin moved shorter distances than when released with distant kin, but this was the opposite for females. This suggested that female dispersal was influenced by intra-sexual kin competition (ie: competition between female relatives for mates), whereas related males may co-operate during reproduction. But the most inbred males dispersed the furthest.

Overall, the researchers felt that the males gained more benefits from further natal dispersion than females.

### **8.2. EXPLODED LEK SYSTEM**

Emlen and Oring (1977) used certain criteria to distinguish mating systems (table 8.1), including the number of mates per male or per female, the presence of resources within a defended territory, and the purpose of female visits to male territories.

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<sup>45</sup> As compared to philopatry, where animals return to their birthplace to breed.

<sup>46</sup> Inbreeding to a point, however, increases the inclusive fitness of the parents. An individual who mates with a relative aids the spread of identical genes in their offspring (Hardouin et al 2015).



(Source: Jimfbleak)

Figure 8.1 - Houdara bustard in captivity in Morocco.

- MALE

1. Monogamy: one partner for breeding season

- a. Mate-assistance monogamy: male assists female in child-rearing
- b. Mate-guarding monogamy: female dispersal

2. Polygyny: one male with multiple females

- a. Female defence polygyny: male defends cluster of females
- b. Resource defence polygyny: male defends resources and females come
- c. Lek polygyny: male defends territory and females come to mate only
- d. Scramble competition polygyny: males find scattered females

- FEMALE

1. monogamy

- a. Female-enforced monogamy: male keeps other females away and assists in child-rearing

2. Polyandry: one female with multiple males

- a. Fertility-insurance polyandry: greater fertilisation of eggs
- b. Better sperm polyandry: genetically diverse sperm
- c. More material benefits polyandry: more resources from males
- d. More paternal care polyandry: more males help in child-rearing

(After Alcock 1993)

Table 8.1 - Types of mating strategy.

A classical lek mating system is "a non-resource-based (or non-economic) mating system, in which females select mates among males that show complex morphological and behavioural traits specifically evolved to attract females" (Morales et al 2001 p86). In other words, males gather in one place to display themselves to females, who choose, mate, and leave. Classical leks are found among bird species like grouse (eg: Black Grouse, Sage Grouse) and birds of paradise (eg: Raggiana Bird of Paradise) (Morales et al 2001). Table 8.2 sums up the costs and benefits of lekking for females.

Benefits	Costs
1. Access to many males to choose mate from rather than having to search for them.	1. Difficulties in choosing because of overwhelming choice, as well as competition from other females or copulation disruption from other males.
2. Greater probability of fertilisation.	2. Increased risk of predation.
3. Ability to assess characteristics that give clues to "good genes" in local population (eg: this is the best available this year).	3. Energy expended to reach lekking site.

Table 8.2 - Main costs and benefits of lekking for females.

Bradbury (1981) identified four characteristics of a lekking species:

- No male parental care.

- Males gather at specific sites to display to females.
- Females take only male genes from the male's "territory" and no other resources <sup>47</sup>.
- Females select mates <sup>48</sup>.

Four theories have been proposed for the development of leks (Morales et al 2001):

i) Males cluster where females are grouped together (ie: high density) (hotspot model) (Bradbury et al 1986).

ii) Females prefer to mate with males at leks (female preference model) (Beehler and Foster 1988).

iii) Females prefer to mate with particular types of males, and subordinate or sub-optimal males take advantage of this (ie: they "parasite" the mating opportunity) (hot spot model) (Arak 1982).

iv) There is a risk of injury if females stay in a male territory, so leks allow the opportunity for mating and nothing more (black hole model) (Clutton-Brock et al 1992).

The North African houbara bustard has a non-classical lek system known as an "exploded (or dispersed) lek system" of mating (Emlen and Oring 1977). Males defend small areas near each other to advertise themselves to females in a lek system, whereas in an exploded lek system there is a considerable distance between the males. The males show high fidelity for their display areas (ie: use the same one in consecutive breeding seasons). Females only visit the males to mate, and their choice of mate is based on the male's quality not resources in the male's "territory" (Hardouin et al 2015).

Most other members of the bustard family (Otididae) have exploded lek systems, but the mating system can vary even within the same species (eg: Great Bustard - classical lek, exploded lek, and monogamy) (Morales et al 2001).

Exploded leks may not fulfil Bradbury's (1981) third characteristic as males may hold large "territories", and because of the distance between displaying males, females

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<sup>47</sup> But resource-based leks are found in insects and some hummingbirds, where males display close to flowers preferred by that species, for example (Morales et al 2001).

<sup>48</sup> Leks allow the display of the best characteristics as the sign of good genes, but females could all choose the same males leading to homogeneity of characteristics in future generations. This is known as the "lek paradox" (Morales et al 2001).

may forage and nest in these areas. Morales et al (2001) pointed out that "a mating system cannot be considered as a lek if male territorial resources explain a part of the variance in male mating success" (p91).

Exploded leks could have evolved from classical leks as "a compromise between the females' interest in having males clustered and the interest of males for avoiding disruptions in highly clumped leks" (Morales et al 2001), or they could be a precursor of classical leks.

Kotrschal and Taborksy (2010) highlighted the problem of classifying mating systems as a resource-based or exploded lek can be similar to a resource-defence mating system, where a male defends a small territory containing critical resources that potential mates are allowed to use.

The key difference is the basis by which females make a choice of quality of genes (lek) versus resources (resource-defence). But Kotrschal and Taborksy (2010) argued that mating systems "may often be better described by their position along a continuum".

These researchers used the example of a cichlid fish (*Simochromis pleurospilus*) in the Zambian part of Lake Tanganyika, to investigate if the primary purpose of male territorial defence was to attract females for mating and/or provide resources. Males defend territories containing turf algae (food), and females spawn on territory before immediately leaving with fertilised eggs. Parental care is provided by female alone via mouth-brooding (Kotrschal and Taborksy 2010).

Eighty-three females were observed in their natural environment (up to 12 m down) for twenty minutes each. All courtship behaviour took place at male territories (evidence for lek), but the females fed at these territories in between courtship (evidence for resource-defence). Kotrschal and Taborksy (2010) concluded that "males appear to generate essential resources for females, which is the key feature of resource-defence mating systems, although the distributions of resources and of males and females are characteristics of an exploded lek" (p1189).

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## **9. SOCIAL BUFFERING**

Social buffering is "the process by which the presence of a conspecific can ameliorate an individual's response to a stressor" (Edgar et al 2015 p11). For example, the presence of the mother reduces the offspring's stress response to an unpleasant stimulus. This is distinct from stress alleviation through social housing (ie: stress is reduced for an individual social animal who is with others before and/or after the unpleasant stimulus (social presence effect) (Edgar et al 2015).

Stress is measured in different ways in social-buffering studies, including heart rate (physiological response) or escape attempt (behavioural response), and the unpleasant stimuli include simulated predation or conditioned association with electric shocks (Edgar et al 2015). Some studies have used social isolation as a stressor, which Edgar et al (2015) saw as a mistake as "changes in behaviour or physiology are likely to reflect a general return to baseline following separation, rather than a social-buffering effect" (p12). Most studies use mammals.

Edgar et al (2015) performed experiments using chickens and found "the first demonstration that avian mothers are able to reduce their chicks' stress responses to an aversive stimulus" (p11). The stressor was air puffs from a canister of inert compressed air for thirty seconds. Fifteen to sixteen day-old chicks experienced this stressor alone or with their mother present. The independent variable was the presence of the mother during the stressful situation. There was also two control conditions - alone or mother present with no air puffs. The experiment used a repeated measures design where each hen's group of chicks performed in all four conditions over two days in a counter-balanced order. The measures of stress were taken from a thermal image of the head (eg: eye temperature reduction during a stress reaction <sup>49</sup> - mean reduction of 1° C after air puffs), and the video-recording of behaviour (eg: reduced preening during stress).

The presence of the mother during the air puffs reduced the stress reaction of the chicks compared to alone.

Social-buffering effects are passive (ie: simple presence of another) and active (ie: changes in the

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<sup>49</sup> This is a sign of stress-induced hyperthermia, where there is an increase in core body temperature and a decrease in peripheral body temperature (Edgar et al 2015).



behaviour of the present individual)<sup>50</sup>. The former was clear in the experiment, but there was evidence of the latter. Differences in the hen's physiological reaction was associated with differences in the buffering effect. The mother's physiological reaction to the air puffs had previously been measured (eg: mean heart rate increase of 62 beats per minute from baseline to post-air puffs), and the hens were aware of what was going to happen to their chicks (ie: conditioned learning) (though the chicks themselves were naive). Edgar et al (2015) noted: "It is therefore not known exactly which aspect of the hens' presence and/or behaviour facilitated the chicks' social buffering. The chicks were unlikely to directly detect their mothers' increase in heart rate, although this cannot be ruled out. Possibly the chicks detected olfactory or temperature changes, a general shift in their mother's behaviour or subtle behavioural or postural changes that were not detected in our behavioural analysis" (pp17-18).

- Hens who received air puffs showed reduced eye and comb temperature, and more time standing alert, but these individuals did not show any such responses when observing air puffs to a familiar adult.
- Thirty-six hens participated in the repeated measures design experiment with one of four conditions each day in a randomised order. The four conditions were:

i) Control - two hens placed in experimental cage with no air puffs.

ii) Control with noise of air puff - Air puffs were directed away from the two hens, so that they could hear the noise of them, but not feel them.

iii) Air puff to conspecific hen - one hen (known as conspecific) received air puffs for thirty seconds while the other hen (known as observer) did not.

iv) Air puff to observer hen - the opposite to the previous condition.

Table 9.1 - Edgar et al (2012).

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<sup>50</sup> Edgar et al (2011) reported "socially mediated arousal" when a mother watched from a distance her chick received air puffs, but this was not evident when watching a familiar adult (Edgar et al 2012) (table 9.1).

## **10. ADAPTATION AND THE URBAN LIFE**

### **10.1 ADAPTATION**

Changing environments can introduce new selective pressures on a species (eg: new type of predator) or the loss of others (leading to "relaxed selection"; Lahti et al 2009)<sup>51</sup>. For example, noctuid moths, no longer preyed upon by bats, do not produce an acoustic startle response (Wund et al 2015).

"Whether or not traits persist, become vestigial, or completely degrade during episodes of relaxed selection depends upon a complex set of factors. These include, but are not limited to, the maintenance of alternative selection pressures favouring trait persistence, correlations with other traits maintained by their own selective agents, the presence and nature of costs associated with trait development and maintenance, the degree to which trait expression is plastic versus constitutive and the rate of mutational decay" (Wund et al 2015 p181). If the original selective pressure is restored, it is known as "reversed selection" (Lahti et al 2009).

If a predator is removed from an environment, and the prey no longer shows a predator-specific behaviour, "does this loss represent the evolutionary (genetic) loss of the capacity to produce the behaviour, the lack of opportunity to learn to produce the behaviour, or some combination of learned and genetic mechanisms?" (Wund et al 2015 p182).

Wund et al (2015) sought to answer this question in a study of three-spine stickleback fish (*Gasterosteus aculeatus*) in Alaska. Fish were taken from four sources - the ocean, and lakes where sticklebacks lived with fish predators, where the predators were absent, and where new predators had been introduced (rainbow trout), as well as laboratory-reared animals originally from these sites. An individual stickleback was placed in a tank and their anti-predator behaviour was measured (eg: freezing, darting, time to resume eating), in response to a simulated trout and bird.

The sticklebacks from different populations responded to predators in different ways. Those from lakes with predators (native or introduced) froze for significantly longer (30 vs 20 seconds) and were slower in resuming eating (80 vs 50 seconds) than sticklebacks used to no predators. This suggested that "relaxed selection leads to a reduction in anti-predator

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<sup>51</sup> There is always the issue of the role of genes and environment on behaviour, and this can be studied in hybridisation (appendix 10A).

behaviour" (Wund et al 2015). But the sticklebacks from trout-introduced lakes showed that "enhanced anti-predator responses can evolve quite quick" (Wund et al 2015).

Wund et al (2015) summed up: "Our results indicate that variation in antiipredator responses to trout attack probably result from a combination of genetic divergence and learning. The overall pattern of differences among predation environments was maintained in naïve, laboratory-bred fish, indicating a strong genetic component. However, responses of these naïve fish were overall lower than the responses shown by their wild-caught counterparts, indicating that experience plays a modifying role in the development of these behaviours. Laboratory-bred fish were also more likely to freeze without an initial dart than were wild-caught fish, suggesting that experience in the wild influences not just the intensity of the response, but also the type of response produced" (p188).

## 10.2. COMMUNICATION

One weakness of acoustic communication is that other sounds compete against the calls made the communicator. In urban areas these sounds are anthropogenic (ie: human noise interference), like traffic noise, and can mask the animal's calls (especially at lower frequency/pitch).

For example, during the breeding season, if a male's call is masked, then he may not be able to attract a female, and/or warn other males off his territory, leading to more aggressive encounters. The same happens if a male does not call at all, or changes his call in response to traffic noise, which females perceive as "low quality" or "incorrect" (Oden et al 2015).

The "acoustic adaptation hypothesis" (Morton 1975) proposed that animals alter or adapt their acoustic communication when there is masking or competition from environmental noise. This is seen in populations of the same species that live in different noise environments (Potvin et al 2011).

Birds have been found to respond to acoustic masking by traffic noise by increased volume (eg: nightingales), changing the frequency/pitch or amplitude of their calls or part of their calls<sup>52</sup>, or reducing the spacing between sounds (ie: more "hurried" songs in cities) and changing the time of day to call (eg: European robins) (Potvin et al 2011). Aspects of the urban environment other than competing noise can have an effect - eg: tall buildings

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<sup>52</sup> The amplitude of the call is important by itself (appendix 10B).

act as reflective surfaces and distort bird song (Potvin et al 2011). "The ability to change specific characteristics of vocalisations likely reflects the learned acquisition of vocalisations" (Oden et al 2015 p473).

Oden et al (2015) found that the calls of the Black-capped Chickadee (*Poecile atricapillus*) and the American Goldfinch (*Spinus tristis*) had higher minimum frequencies in areas of high traffic noise, but maximum frequencies did not change (table 10.1). Lower pitches of calls are more likely to be masked by traffic noise. Both species use their calls for individual recognition, and are highly vocal outside the breeding season. The researchers made recordings of calls in eastern Nebraska, USA, close to a four-lane interstate highway (high traffic noise) and away from empty country roads (low traffic noise). Over 3200 calls were recorded in November-February 2011-12 and 2012-13 at twenty sites.

	High traffic noise	Low traffic noise	Significance
Chickadee: Minimum Maximum	3.1 4.1	2.9 4.2	p = 0.009 ns
Goldfinch: Minimum Maximum	3.1 4.3	2.9 4.4	p = 0.03 ns

(ns = not significant at  $p < 0.05$ )

(Based on Oden et al 2015 figure 2 p476 and figure 3 p477)

Table 10.1 - Approximate means (kHz) of minimum and maximum frequency of calls recorded.

Potvin et al (2011) recorded the male songs of silvereyes (*Zosterops lateralis*) (figure 10.1), a common bird in Australia, at fourteen paired urban and rural sites in south-east Australia. The frequency range of the songs was 2-6 kHz (of which 1-4 kHz was vulnerable to traffic noise masking). The birds raised the lowest frequencies of their songs (which are learned) and contact calls (which are innate) in urban areas. The change in contact calls suggested to the researchers that "urban habitats directly influence the evolution of vocalisations by selecting for genetic changes in vocal patterns or ability" (Potvin et al 2011 p2468).

The speed of the song (syllable rate) decreased in urban environments, which was "consistent with the hypothesis that reflective structures degrade song and encourage longer intervals between syllables" (Potvin et al 2011 p2464).



(Source: Benchill)

Figure 10.1 - Silvereyes.

Potvin et al (2011) explained it thus: "One hypothesis is that buildings and urban areas may act like canyons, degrading intricate syllables through reverberation, and blending separate song elements. By increasing the temporal separation of syllables, silvereyes may be able to communicate these syllables more effectively... It seems reasonable to expect that under urban conditions, information contained in faster or more complex songs may be lost because the syllables are not only degraded by the physical properties of the environment, but may also be masked by high levels of noise. Song and syllable complexity are important indicators of male attractiveness and/or quality in many birds. High syllable rates may be energetically or physiologically costly to maintain, and thus individuals might reduce the cost and increase the effectiveness of their vocalisations by slowing songs down and in the process, communicate song complexity more effectively" (p2468).

### 10.3. LIVING CONDITIONS

European rabbits (*Oryctolagus cuniculus*) are declining in some rural areas but thriving in urban ones (Ziege et al 2015), making it an "urban adapter" or "urban exploiter" (McKinney 2002).

Ziege et al (2015) compared the burrows of rabbits in nine parks in the city of Frankfurt am Main, Germany, four parks on the outskirts, and three adjacent rural areas. The number of rabbits in a burrow was determined by observation, and by sending ferrets into the burrows to chase rabbits out. Group sizes declined with the degree of urbanity (eg: amount of artificial ground cover like streets) (negative correlation:  $r = -0.61$ ;  $p < 0.001$ ), while burrow densities (ie: number of burrows in an area) increased with increased urbanity (ie: positive correlation:  $r = 0.77$ ;  $p < 0.001$ ).

Ziege et al (2015) offered the following possible explanations for smaller groups in the city:

i) Larger groups have less per capita energy loss during cold periods, but cities tend to be warmer than the countryside.

ii) Large burrows with many entrances are better as a protection against predators, while urban environments may well have less predation risks.

iii) Large social groups are formed when resources are limited, but this is not the case in cities.

However, the researchers admitted that it was not clear if urbanisation caused the smaller groups and burrows, or whether smaller groups moved to cities.

### 10.4. RECOGNISING INDIVIDUAL HUMANS

Prey animals use cues their predator to assess immediate risk. These cues include the distance of the predator away (eg: encoded in meerkat alarm calls), and whether the predator is hungry or not (eg: fish and insect) (Davidson et al 2015).

Direction of predator gaze is also an important cue to the likelihood of attack. For example, basking black iguanas use it in the decision to flee, while jackdaws do not approach an area where the predator is looking (Davidson et al 2015).

In the case of animals that live near to human "predators", can they recognise individuals as well as their direction of gaze? Certainly, recognition of individual humans has been reported in Gunnison's prairie dogs (based on differences in alarm calls) (Slobodchikoff



et al 1991), for instance, and birds, like magpies, attack particular individuals approaching their nest (Davidson et al 2015) <sup>53</sup>.

Davidson et al (2015) observed that "if prey benefit from assessing predator risk through individual recognition, they may also benefit from assessing predator risk based on where the predator's gaze is directed (ie: towards the prey or elsewhere)" (p18). These researchers studied jackdaws (*Corvus monedula*) (figure 10.2), who, in captivity, are known to distinguish between familiar and unfamiliar humans, and to respond aversively to direct gaze from the latter (eg: von Bayern and Emery 2009).



(Source: David Castor; in public domain)

Figure 10.2 - Jackdaw.

Using a wild nestbox population close to the University of Cambridge in the 2013 breeding season, Davidson et al (2015) tested three one-tailed hypotheses:

1. If jackdaws can recognise individual humans, they will respond more defensively to a threatening than neutral (non-threatening) individual.

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<sup>53</sup> Common honeybees have been trained to recognise pictures of human faces (Tibbetts and Dyer 2013).

2. If jackdaws pay attention to the gaze of the human, they will respond more defensively if the gaze is directed towards them than away.

3. Combining the above hypotheses, jackdaws will respond more defensively to a threatening individual gazing at them than a neutral individual gazing away.

For convenience, the researchers wore latex full-head masks during the experiment - a "threatening" mask when the nestbox was disturbed (ie: weigh chicks) and a "neutral" mask when the human walked near the nestbox. Once of each of the first three days after hatching. the adult jackdaws in eight nestboxes experienced the two masks before the experimental trials. There were two independent variables (type of mask and direction of gaze) giving four conditions <sup>54</sup> in this repeated measures design over four days. The researcher in the mask sat thirty metres away from the nestbox for forty minutes.

The dependent variable (speed to return to nestbox, perch outside, and enter) was scored from video recordings of the birds by researchers blind to the experimental condition.

The first hypothesis was supported. Jackdaws were significantly quicker to return to the nestbox in response to the human in the threatening mask than the neutral one (1000 vs 1400 seconds). There was no significant difference in relation to the other two hypotheses, but the second hypothesis had a non-significant difference: "Once jackdaws made contact with the box, they tended to be quicker to enter when the experimenter was looking towards the box rather than away" (Davidson et al 2015 p20).

The findings showed that the wild jackdaws, who live near humans, could distinguish individual human appearance as threatening as not.

## **APPENDIX 10A - HYBRIDISATION**

Hybridisation is the combination of two closely related species. Schieltz and Rubenstein (2015) noted: "In any species pairing, the effect of hybridisation on phenotype can be quite variable depending on the levels of genetic introgression and differences in gene expression. Particular traits may be determined by one parent only, or be intermediate between the two. Hybrid individuals generally possess physical characteristics of both parents, while behaviour may vary depending on the complexity of gene interaction and the extent to which

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<sup>54</sup> (1) Threatening mask and gaze at; (2) Threatening mask and gaze away; (3) Neutral mask and gaze at; (4) Neutral mask and gaze away.



behaviours are learned from one species or the other. Studying hybrid behaviour can, therefore, be an opportunity to separate environmental or learned traits from genetic ones" (p17).

For instance, Alberts and Altmann (2001) observed the hybrids of yellow and anubis baboons in Kenya for over thirty years. Hybrid males who were raised in a yellow baboon social group left at a younger age than yellow males (which is a trait of anubis males). This suggested the influence of genes over environment for this behaviour.

Schieltz and Rubenstein (2015) studied the natural hybridisation of the plains zebra (*Equus quagga*) and the Grevy's zebra (*Equus grevyi*) in central Kenya.

Schieltz and Rubenstein (2015) stated:

Because they [hybrids] are born to plains zebra mothers, hybrids have been raised exclusively in the plains zebra society. If social behaviour is the outcome of only learning and not influenced by genetics, we would expect hybrids to behave just like plains zebra, because hybrids have virtually no interaction with Grevy's zebras... work on hybrids of other species suggests that genetics can play a role in determining social behaviour. Therefore, if genetics is the primary determinant of the behaviour of hybrids, we predicted that hybrids would display behavioural phenotypes intermediate to the two parents and show some behavioural characteristics of Grevy's zebras. Each individual hybrid may show behaviour more strongly resembling one parent or the other, depending on their unique genetic make-up and the relative contribution of genetic material from each parent. In either case, if these behaviours are determined by genetics alone and not modified by learning, then they should be fixed from birth and not change over an individual's lifetime (p19).

Animals were observed over three months in 2006 and 2010 at Ol Pejeta Conservancy in Laikipia District, Kenya. The hybrids showed Grevy's zebra-like behaviours (which supports the role of genes) as well as being reasonably integrated into the plains zebra groups (support for environment and social learning).

Hybrid females appeared to show subtle differences (eg: more vigilant than plains females and equivalent to Grevy's). Hybrid males displayed more obvious differences.

They were significantly less likely to be the stallion with a harem than plains males, and significantly more likely to be alone. Plains males have a harem (a stable group of a stallion with several exclusive females and dependent offspring) which are defended. Lone grevy's males defend a territory around resources and attempt to control females in their territory (unstable group).

Schieltz and Rubenstein (2015) summed up their findings: "In some cases, hybrid behaviour was intermediate to the two parents, in other cases it more closely resembled one parental equid type or the other, and in the case of age of dispersal, it differed from both parental species. However, at least for males, behaviour also does not appear to be the result of only genetics. Behaviours are not set from birth but can change over time, and we suspect they may be modulated by positive and negative reinforcement, suggesting a strong (gene) environment interaction. Therefore, we believe that it is this interaction of genes and environment over time that ultimately shapes behaviour of many hybrids" (p25).

## **APPENDIX 10B - LOW-AMPLITUDE SIGNALS**

Acoustic communication can use high-amplitude (loud) signals, which cover long distances, and quieter (low-amplitude) ones <sup>55</sup>. The latter are soft songs or whispers, for example, and are defined as signals "produced at amplitudes that limit the signal's active space to either a single receiver or a group of receivers close to the signaller" (Reichard and Anderson 2015 p255) <sup>56</sup>.

Low-amplitude signals can be a quieter version of a loud signal ("soft long-range song"), but also an acoustically distinct signal ("short-range song"). For example, male Pacific field crickets (*Teleogryllus oceanicus*) produced the latter when close to receptive females (Reichard and Anderson 2015) <sup>57</sup>.

Female birds, for instance, seem to prefer louder male songs, based on preference experiments which play courtship songs at two different amplitudes, each at a different end of the cage and see where the female goes (eg: red-winged blackbirds, zebra finches) (Zollinger and Brumm 2015).

Low-amplitude signals are used in close-range mating displays (eg: "quiet squeals" by both sexes of Mandarin voles during sexual behaviour), intra-sexual competition (usually male-male), close to group members (eg: contact maintenance), alarm calls, and parent-offspring interactions (eg: begging calls of some birds) (Reichard and Anderson 2015).

These functions are also achieved by loud calls, so

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<sup>55</sup> Technically, signal amplitude at position of receiver (or signal-to-noise ratio) (Zollinger and Brumm 2015).

<sup>56</sup> The detectability of a signal can vary by loudness, contrast to other sounds in the environment, and its predictability (eg: signalling from one position or from a variety) (Reichard and Anderson 2015).

<sup>57</sup> Acoustic signalling by insects and other arthropods is typically non-vocal (ie: produced by muscle contraction and exoskeleton, and not the vocal tract) (Balenger 2015).

why have soft signals evolved? <sup>58</sup> One answer is the "eavesdropping avoidance hypothesis" (Dabelsteen et al 1998) <sup>59</sup>. Any acoustic communication can be heard by individuals not meant to be the receiver of the signal (ie: eavesdropper). This is a cost of acoustic communication (table 10.2). Quieter communication reduces this cost, particularly in areas of high density of predators. For example, birds that suffer high rates of nest predation have evolved quieter begging calls by the chicks. While in areas with conspecific eavesdroppers, low-amplitude signals during courtship avoid the cost of another male being attracted (Reichard and Anderson 2015) <sup>60</sup> <sup>61</sup>.

Reichard and Weiklin (2014) reviewed the work on soft calls in 749 species of birds, and concluded that "low-amplitude vocalisations are not simply less intense variants of high-amplitude vocalisations but structurally and functionally distinct types" (Gustison and Townsend 2015 p282).

Male birds respond more aggressively to a louder singing male territorial intruder than a quieter singing one <sup>62</sup>. For example, Brumm and Ritschard (2012) simulated territorial intrusion with a stuffed model chaffinch (*Fringilla coelebs*) and speakers which played either a low- or high-amplitude song to the territory-holder. The latter chaffinch sang less and approached the intruder closer (signs of territorial aggression) to the louder singing "intruder" <sup>63</sup> <sup>64</sup>.

Reichard and Anderson (2015) stated: "Collectively, pressure from eavesdroppers fails to explain low-amplitude signalling in all contexts. There is currently greater empirical support for the role of eavesdropping

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<sup>58</sup> "One particularly intriguing aspect of low-amplitude signals is that their meek form seems antithetical to two of their dominant functions: to impress potential mates or to threaten rivals" (Anderson and Reichard 2015).

<sup>59</sup> Eavesdropping another species can have advantages (appendix 10C).

<sup>60</sup> Acoustic eavesdropping by conspecifics is seen in satellite male crickets who exercise "adaptive silence" (Conner 2014). These males do not sing, but wait close to loud singing males to intercept any approaching females. "One advantage to this behaviour is that it results in some savings of energy, particularly when competition is high. However, satellite behaviour is also beneficial for males from the many populations of field crickets that are subject to acoustically orienting predators and parasitoids" (Balenger 2015 p279).

<sup>61</sup> Balenger (2015) pointed out that quiet calling is "a prevalent phenomenon" among birds as more than half of species in North America are reported to use it.

<sup>62</sup> But Akcay et al (2015) felt that low-amplitude calls were the best predictor of impending attack in many bird species.

<sup>63</sup> Searcy and Beecher (2009) proposed three criteria for establishing that a call is a threat signal:

- i) Context - the call increases during aggressive interactions.
- ii) Response - the receiver responds as if it is a threat call.
- iii) Predictive - the call comes before aggression if the receiver does not withdraw.

<sup>64</sup> For males in vocal contests with other males, being overheard by females can be an advantage as the females could choose the winner (Akcay et al 2015).

predators than for eavesdropping conspecifics in driving the evolution of low-amplitude signals" (p259) <sup>65</sup>. While Zollinger and Brumm (2015) felt that "social aggression is likely to pose a stronger constraint on song amplitude than metabolic costs, and that it could function as an inverse selective force to female preferences that favour loud song" (p294).

COST	DETAILS
Energy	More energy expended by louder calls (possibly).
Courtship disruption	Rival males (usually) interfering/competing during courtship/mating.
Predation	Predators that locate prey by hearing prey's calls.
Parasitism	Parasites that locate hosts based on host's calls.

Table 10.2 - Costs of loudness of calls.

Akcay et al (2015) listed other explanations for the evolution of soft calls (specifically as threat signals by birds):

i) Readiness hypothesis - Visually tracking a competitor is affected by bill movement when calling, and males getting ready to fight move their bill a little as in a soft call, so as not to interfere with visual tracking. Akcay et al (2015) admitted that this hypothesis had "not yet been subjected to critical tests".

ii) Competing functions hypothesis - Soft calls are ineffective at discouraging territorial intruders, say, and lead to more fights than loud calls. Based on the handicap principle, the strongest males can afford the cost of fighting every time. The handicap principle suggests that males show-off their good genes by making their lives very difficult. But threat calls are often a mixture of loud and soft calls, which challenges this hypothesis (Akcay et al 2015).

iii) Vulnerability handicap hypothesis - Similar to the previous hypothesis, the cost of soft calls (ie: their ineffectiveness) has evolved as a honest signal of a highly motivated signaller.

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<sup>65</sup> But Searcy and Nowicki (2006) found no support for predator eavesdropping avoidance. Song sparrows were played the call of a territorial intruder or an intruder and a predator. Soft calls increased in the former condition, which is opposite to predicted (Akcay et al 2015).

"A logical difficulty for this hypothesis is that the amplitude of an auditory signal always decreases with increasing distance from the source; consequently, high amplitude, not low amplitude, indicates close proximity... Experiments with birds (and humans) have shown that signals with lower amplitude are indeed interpreted as having originated at a greater distance, rather than a closer one" (Akçay et al 2015 p270).

iv) Receiver retaliation hypothesis - Soft calls provoke aggression in the receiver as well as retreats, and as long as there is a balance of these two behaviours, low-amplitude calls for stronger signallers can be an honest signal.

Some moths produce a low-amplitude courtship song and no other acoustic communication, while some crickets (eg: Oceanic field cricket, *Teleogryllus oceanicus*) have calling songs that contain high- and low-amplitude elements (Balenger 2015).

An example of the former is the Asian corn borer moth (*Ostrinia furnacalis*). Males produce ultrasonic sounds by the stridulation of specialised wing and thorax scales which can only be detected by the female 3 cm away. It causes the receiver to freeze (as in avoiding bat detection) and the male takes the opportunity to mate with the stationary female (Nakano et al 2010).

Gustison and Townsend (2015) brought together studies of 534 adult calls from 47 species of mammals. The researchers categorised low amplitude calls as below 90 dB, medium amplitude as 90-95 dB, and above 95 dB as high amplitude calls. The context of calling, gender of the caller, and details about the calls (eg: duration) were distinguished.

Of the 534 calls, 109 (20%) were classed as low-amplitude, 290 (55%) as medium, and 135 (25%) as high-amplitude. This highlighted that "medium-amplitude calls and calls with no clear description of amplitude are common calls types in the vocal repertoires of mammals" (Gustison and Townsend 2015 p285).

High-amplitude calls were most common in the context of competition and predator alarm, and low-amplitude calls in affiliative social contexts like grooming, but there was no association between the latter and mating contexts.

Gustison and Townsend (2015) felt that their research "raises the intriguing possibility that low-amplitude calls can serve multiple functions, and as such, may constitute a more influential class of vocalisations in the daily lives of mammals than previously assumed" (p287).

## Reliability of Signal and Faking

The reliability of a signal is important (ie: it is a honest signal). Loud communication is seen as difficult to fake because of the physical requirements on the signaller to make such sounds <sup>66</sup> <sup>67</sup>. For example, male birds can vary between 5-15 dB in a given population, and a bird would need to increase its vocal sound pressure nearly six times between the quietest and loudest. "If this variation in song amplitude is linked to some fitness-related trait in males, females could use amplitude to assess the quality of potential mates" (Zollinger and Brumm 2015 p290). But this is not necessarily true - larger birds do not always make louder noises (eg: rock sparrows) (Zollinger and Brumm 2015).

Soft communication does not have the physical "barrier" (production costs), which means that it is vulnerable to faking. But, in some birds, the honesty of a soft song is supported by an attack in an aggressive interaction (ie: not a bluff) (Reichard and Anderson 2015).

One way to stop faking is to make the soft signal complex, which imposes costs on the signaller. For example, Hack (1998) found that a male house cricket (*Acheta domesticus*) consumed two and a half times more oxygen when producing the complex low-amplitude courtship song than a simpler high-amplitude calling song. But "males also produce a visual courtship display (ie: rocking back and forth in place) that may account for some of the increased respiration" (Reichard and Anderson 2015 p260).

Zollinger et al (2011) found no significant increase in oxygen consumption by zebra finches when singing quiet or loud songs (25 dB difference). The researchers designed a respirometry mask to cover the head of the bird which measured oxygen consumption, and was fitted with a microphone. Loud songs were elicited by playing white noise. Zollinger and Brumm (2015) observed: "This does not mean that birds can increase their vocal amplitudes at no energetic cost. A metabolically cost-free increase in vocal power would be epistemically impossible because it violates the laws of thermodynamics. Louder song requires significantly greater sub-syringeal airsac pressure..., which is likely to be produced by an increase in respiratory muscle activity... Increased muscle activity should

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<sup>66</sup> For example, size (eg: frequency of calls of frogs), and energy (eg: drumming display of spiders) (Akçay et al 2015).

<sup>67</sup> Akçay et al (2015) noted a surprising finding from studies on song sparrows - more under-signalling than over-signalling. Under-signalling is where a strong individual signals weakly, which is dishonest communication in one sense, but it is not expected compared to over-signalling (a weak individual pretends to be strong). This observation could fit with the eavesdropping avoidance hypothesis.

necessarily result in some additional metabolic costs, but any such increase required even for large increases in vocal amplitude were so small as to be undetectable above the background metabolic consumption..." (p293).

Cheng (1992) referred to the idea of autocommunication or self-stimulation, which low-amplitude signals may achieve. For example, female ring doves produce a quiet "coo" sound that alters its reproductive hormone levels rather than communicates to a male, while domestic cats have a quiet purr after stress to soothe themselves (Reichard and Anderson 2015).

Reichard and Anderson (2015) observed: "In general, autocommunication represents an intriguing but often overlooked explanation for why animals produce acoustic signals, particularly when those signals are low amplitude and only heard by the signaller and a small number of potential receivers" (p260).

Research on low-amplitude signals in songbirds and insects, for instance, is limited by having the equipment to record it (as well as particular sounds falling outside the human hearing range). For example, the close-range courtship song of a moth may be as low as 3 dB sound pressure level (SPL) at one metre away (Reichard and Anderson 2015).

"Signal transmission is influenced by environmental acoustics due to absorption of and scattering by vegetation and others reflective surfaces in the habitat, air temperature and humidity, and fluctuations of signal amplitude induced by wind. Therefore, the researcher must take all these variables into account when trying to measure sound amplitude" (Zollinger and Brumm 2015 p289).

## **APPENDIX 10C - EAVESDROPPING ANOTHER SPECIES**

Eavesdropping on alarm calls by different species with a shared predator (ie: heterospecific alarm calls) has been reported in about seventy species, including birds on birds, mammals on mammals, mammals on birds and vice versa, and even lizards eavesdropping on birds (Murray and Magrath 2015).

But there are limitations to such eavesdropping, including (Murray and Magrath 2015):

i) The eavesdropper may lack the "species-specific perceptual specialisations" (eg: ability to discriminate calls).

ii) Heterospecific calls can be unpredictable in terms of direction of source, say, which restrict detectability.

iii) The eavesdropper may only detect part of a signal.

iv) The eavesdropper may lack familiarity with a call.

These limitations means that "eavesdropping will become particularly difficult when signal quality or signalling conditions are poor, such as when calls are of low amplitude, degraded during transmission, or when there is a low signal to noise ratio" (Murray and Magrath 2015 p34).

Murray and Magrath (2015) studied the eavesdropping of White-browed scrub-wrens (*Sericornis frontalis*) and superb fairy-wrens (*Malurus cyaneus*) in a playback experiment around Canberra, Australia. Both birds are vulnerable to the same flying predators (eg: collared sparrowhawks), and produce similar aerial alarm calls. However, there are differences in the calls in, for example, the peak frequency.

It is known from other research that both species respond to each other's calls under ideal conditions (Magrath et al 2007), but this appears to be a learned behaviour. For example, fairy-wrens not living near scrub-wrens do not respond to the latter's calls (Magrath et al 2009).

Murray and Magrath (2015) played alarm calls from conspecifics or heterospecifics to fifteen groups of each species, while varying the amplitude (signal attenuation) (medium or low) <sup>68</sup>, and the signal degradation (unaltered recording - undegraded or degraded <sup>69</sup>). This was a repeated measures design with eight experimental conditions (table 10.3), and a control condition with a parrot contact call.

		Own species	Other species
Low amplitude	Undegraded	1	2
	Degraded	3	4
Medium amplitude	Undegraded	5	6
	Degraded	7	8

Table 10.3 - Eight conditions in playback experiment.

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<sup>68</sup> Low amplitude makes it more difficult to eavesdrop the whole call with its different elements.

<sup>69</sup> The degraded version was recorded fifteen metres away through dense vegetation. With a degraded signal, a "greater difficulty of reception would increase the chance of missed detections or false alarms..., potentially making eavesdropping a poor source of information" (Murray and Magrath 2015 p35).



The birds were observed for five minutes of undisturbed feeding before a playback. In response to the playback, fleeing to cover or not was scored.

Overall, the birds were more likely to flee to conspecific than heterospecific calls, but they did flee to heterospecific calls at natural (medium) amplitude. Degradation had no effect on response to conspecific calls (ie: always flee), but did on heterospecific ones (ie: not flee).

Murray and Magrath (2015) summed up: "Our results provide partial support for the idea that eavesdropping on heterospecific signals is harder than receiving alarm calls from conspecifics, in part because of signal attenuation and degradation... We suggest that alarm call degradation had little effect on conspecific communication because listeners use specific acoustic features that are resistant to degradation. By contrast, it may be harder to cope with heterospecific call degradation in part because individuals must learn to recognize specific call variants" (p38).

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