

11. CHEMICAL DEFENCES AGAINST PREDATORS

Prey can protect themselves at different points in the prey-predator interaction (appendix 11A) (Jeschke et al 2008):

1. Prevent predator's search
2. Prevent encounter with predator
3. Prevent detection by predator
4. Prevent predator attacking
5. Prevent consumption by predator.

Chemical defences/weapons, of which there are many varied types (table 11.1), are particularly useful in stages 4 and 5. Defensive chemicals are used to reduce the risk of bodily harm, and are usually poisons (Berenbaum 1995)⁷⁰.

- Exploding defender - eg: ant abdomen explodes sticky secretion⁷¹.
- Squirting blood - eg: Texas horned lizard.
- Stinking jets - eg: skunk.
- Repellent clouds - eg: sea slug.
- Scalding bombardments - eg: bombardier beetle.
- Spraying acid - eg: wood ant (formic acid).
- Gurgling foam - eg: tiger moth in South Africa.

(Source: Attenborough 1992)

Table 11.1 - Examples of chemical defences/weapons.

In understanding chemical defence, there are three issues to consider (Parejo et al 2013):

i) The origin of the defensive substance - is it produced by the organism or obtained through the prey it eats, for example?

ii) The chemical composition of the defensive

⁷⁰ Chemicals can also be used defensively in other ways - eg: chemical disguise by social parasites (appendix 11B).

⁷¹ A carpenter ant species from south-east Asia (*Camponotus (Colobopsis) cylindricus* complex; COCY) "explodes" as a defence strategy. A COCY worker grabs an intruder and suicidally releases a glandular product which is adhesive producing "a permanent 'death grip'". Voluntary self-sacrifice in defence of territory by internal rupture is known as autothysis (Davidson et al 2012) (or abdominal dehiscence; Shorter and Rueppell 2012).

Autothysis has also been reported in some termite species (eg: *Globitermes sulphureus*). "In all cases, the released substance is sticky and binds to predators, congealing when exposed to air and causing distress, immobility, or death to the target" (Shorter and Rueppell 2012).

Autothysis is a form of self-sacrifice behaviour used by eusocial insects, which also includes sting autotomy (self-amputation of stinger and poison sac), and altruistic self-removal by infected individuals (Shorter and Rueppell 2012) (appendix 11C).

chemical.

iii) The effect of the chemical defence on predators.

Chemical weapons are often secondary compounds derived from metabolites not involved in primary physiological processes (Berenbaum 1995).

Chemical defences are rare in organisms at the top of the food chain (eg: large vertebrates that have size, speed and strength), and more common in organisms with limited movement (eg: marine invertebrates) (Berenbaum 1995).

Texas Horned Lizard

Blood-squirting from the eyes (or nose) ⁷² is an anti-predator strategy used by the Texas horned lizard (*Phrynosoma cornutum*) (figure 11.1) towards canids (eg: coyotes) ⁷³.



(Source: The Sackinator; in public domain)

Figure 11.1 - Texas horned lizard.

Sherbrooke and Middendorf (2001) investigated this behaviour with forty adult Texas horned lizards and five

⁷² Ocular-sinus squirting.

⁷³ Not all species of horned lizard blood-squirt - eg: round-tailed horned lizard (*Phrynosoma modestum*) does not (Sherbrooke and Middendorf 2001).

juveniles collected in Arizona and New Mexico, USA. A pet Labrador was used as the "predator", and it was encouraged to "interact" with an individual lizard (ie: bark, paw, gentle bite, or pick up). As soon as eyelid swelling/"eye puffiness" or blood-squirting was observed, the lizard was picked up by a researcher. A total of 1085 squirts were observed in 151 trials over seven days of repeated daily testing. Over 80% of the adult lizards squirted at least once, and two lizards squirted on all seven days. Three of the five juveniles squirted. Blood-squirting had a cost with up to 7% loss of body mass for some individuals over all the trials.

Sherbrooke and Middendorf (2001) summed up: "Without the use of a blood-squirting defence and its presumed delivery of noxious chemicals (which may be contained in circulating as well as squirted blood...), a horned lizard may have little chance of surviving an encounter with a canid, because both coyotes and kit foxes... eat *Phrynosoma cornutum*. With a blood-squirting defence a lizard's survival chances increase, probably substantially... The physiological costs of the defence, in terms of blood loss, can be low or high. The success of this defence behaviour depends on factors such as the efficacy with which squirted blood is delivered to membranes in the mouth of the predator... and the experience and hunger state of the individual canid" (p1121).

Coyotes (*Canis latrans*) (figure 11.2) show a startle response and/or avoidance response to blood-squirting. Sherbrooke and Mason (2005) found that "this blood affects oral receptors, causing a negative response in coyote attack behaviour that potentially increases survival of the lizards" (p216). Captive-raised adult coyotes were tested in staged interactions with Texas horned lizards, and in experiments, where blood was squirted by the researchers into three different areas of the coyote's face (eyes, nose, mouth). There was a negative response (eg: lateral head-shaking, jaw gaping or tongue licking) to the blood of the Texas horned lizard which was not found in response to a saline solution or the blood of spiny lizards. This suggested that the coyotes were responding to a compound in the blood of the Texas horned lizard (ie: blood-borne chemical) (which targeted taste receptors in the mouth) (Sherbrooke and Mason 2005).



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

Figure 11.2 - Coyote.

Bombardier Beetle

Beetles need time to unfurl their wings in order to fly, but in emergencies they do not have this time. Thus the use of a strategy to "buy time" when under attack (Eisner and Aneshansley 1999).

The bombardier beetle accurately aims the substance, which is hot (100 °C), and the discharge includes an audible detonation. The substance (quinone) is generated explosively at the point of firing by mixing two sets of chemicals stored in separate glands (the reservoir or storage chamber and the reaction chamber) (Eisner et al 2000). A bombardier beetle can discharge nearly twenty times on one occasion before depletion (Eisner and Aneshansley 1999).

They can spray in all directions, with considerable efficiency, and this can include drenching itself (and withstanding the heat) (Eisner and Aneshansley 1999).

Skunks

Skunks spray a strong-smelling musk from anal glands that can cause nausea, burning sensations to the eyes, and irritation to the skin, but this is a last resort after the failure of other anti-predator strategies⁷⁴. These strategies, in order, are tail-up (communicating alertness to predators), run, stomp, charge, den (avoidance behaviours), scratch, hide, hiss (warnings of noxiousness), aim the anal glands, and spray (Medill et al 2011).

Medill et al (2011) charted the development of these strategies by raising seventy striped skunks (*Mephitis mephitis*) (figure 11.3) from birth to 52 days old in Manitoba, Canada. The anti-predator behaviours were elicited by handling the animals, and all behaviours were present by 32 days old.

Tail-up was evident first, at seven days old, and stomp at 17 days, with aim, bite and hiss at 22 days old.



Run and hiding at 27 days, and, finally, scratch appeared. Musk was present at seven days old, and non-direct spray was observed at 17 days, with direction appearing between 32-42 days old.

Spraying was used more by these juveniles than adults, and this fits with the fact that juvenile mortality risk is greater than adult risk. Thus, "juvenile skunks may be more likely to spray as a direct result of their greater vulnerability" (Medill et al 2011 p46). Adults, though, "benefit from conservative use of their chemical compounds as they reduce energetic costs and avoid depletion of the chemicals" (Medill et al 2011 p47).

(Source: pdimages.com; in public domain)

Figure 11.3 - Striped skunk.

⁷⁴ Skunks face many different predators, including owls and eagles, badgers, foxes, and coyotes (Medill et al 2011).

Marine Molluscs

The skin and mucous of sea snails contains distasteful compounds which discourage eating, while some marine gastropods have skin glands that secrete acids, like sulphuric acid (Derby 2007).

Sea hares (*Aplysia californica*) release compounds when attacked by spiny lobsters, which include aversive substances, and stimulate or inhibit feeding behaviour. The ink secretion is treated as food in some situations, or produces escape responses in others (Derby 2007). While food pellets treated with chemicals from the mucous secretion of the sea slug (*Haminoea cyanomarginata*) was rejected by a predator shrimp (Mollo et al 2008).

Cephalopods produce ink secretions as clouds and pseudo-morphs. The latter are "well-defined objects composed of ink and mucous. They keep their form and physical integrity for some time after release by the cephalopod, and they can be almost as large as the animal releasing them" (Derby 2007 p281). They are a distracting decoy. The cloud is similar, as in the "Black-Ink-Jet manoeuvre", where "a squid changes its colour (from dark to light, or light to dark) and at the same time moves quickly away and releases ink, thus giving a would-be predator the illusion that the cloud of ink is the squid while the 'invisible' squid disappears" (Derby 2007 p281).

Chemicals released by attacked marine gastropods can act as alarm signals to neighbouring conspecifics, and other species (eg: sea hares respond to ink from octopus and squid).

Derby (2007) summed up the findings from the study of the chemical defences of sea hares:

- A mixture of chemicals are used.
- The compounds are produced by the organism or diet-derived (eg: from algae).
- The chemicals influence a single predator in several ways (eg: deceive and warn).
- Different compounds work for different predators.
- A chemical may be used in different ways (eg: in ink or on eggs to discourage consumption).

Nestling Vomit

Chemical defence by birds is rare, but Parejo et al (2013) reported an odorous orange substance regurgitated by the nestlings of the Eurasian roller (*Coracias garrulus*) (figure 11.4) when threatened. Such vomiting behaviour is not common among nestlings of different species, and it is costly in terms of loss of bodily

fluids. It has been observed that roller parents returning to a nest where there is a smell of vomit are more cautious (Parejo et al 2012), which would suggest that they understand it as a predator defence.



(Source: Gould 1837; in public domain)

Figure 11.4 - Drawing of roller.

Parejo et al (2013) studied rollers in nest-boxes, that contained about five nestlings at a time, in south-eastern Spain between 2008 and 2012. Four aspects of the vomiting behaviour were studied:

i) The stimulus that induced vomiting - A researcher approached the nestling and used four different stimuli: speak loudly (auditory stimulus), show face (visual), touch gently (tactile), and pick up (mobile stimulus). All forty-three nestlings tested vomited in response to being picked up. This would fit with the main predators who try to grasp the nestlings, namely snakes who constrict while holding them with the mouth.

But this may not stop other predators. Parejo et al (2013) said: "As nestlings only vomit after being grasped and moved, some of the common predators of hole-nesting birds, as rats and mustelids [eg: weasels], must perhaps bite a nestling roller before realising that the prey is unpleasant. Thus, one could wonder about the nestling advantage of this defence. Kin selection is a possible answer to that question because a predator that finds the first nestling of a brood of five to be distasteful may leave alive the others. Alternatively, the advantage might be found in parental fitness because parents would benefit from an incomplete predation event at their nest".

ii) The origin of the vomit - Nestlings aged 7-20 days old (the peak for vomiting) were deprived of food for one hour to see if this reduced the production of vomit (ie: food-based as opposed to glandular-based). The deprivation of food was achieved by placing a neck collar on the nestling that stopped swallowing but not vomit production. Twelve of the fourteen nestlings with neck collars reduced their production of vomit over the hour compared to only four from a comparison group.

The main prey for rollers are grasshoppers and beetles which acquire chemicals from plants which they use as their chemical defence. "Many herbivorous insects such as grasshoppers regurgitate when disturbed. The defensive role of the expelled fluid has been attributed primarily to ingested plant secondary compounds. Grasshoppers are the main prey that rollers hunt to feed their nestlings... Furthermore, rollers feed their offspring with a large share of poisonous arthropods that are avoided by most of the other sympatric insectivorous birds. This suggests that rollers are resistant to these toxic substances and could have the ability to sequester chemicals from their protected prey to defend themselves, like phytophagous insects do with plants secondary compounds" (Parejo et al 2013).

iii) The chemical compounds in vomit - Hydroxybenzoic and hydroxycinnamic acids were the main

chemicals found in vomit samples. These chemicals are found in the leaves of local plants which are eaten by insects (eaten by rollers).

iv) The effect of the vomit - Twenty dogs were offered meat smeared with roller nestling vomit and meat smeared with water, and eighteen of them preferred the latter. Parejo et al (2013) said: "It should be acknowledged here that despite the initial avoidance that dogs showed against meat with vomit, many dogs finally ate it. However, they did that after some minutes, perhaps after the volatilisation of much of the smell of the vomit. This fact probably means that vomiting only serve in the short time against predators because of the volatile nature of the expelled substance. Nevertheless, it is interesting to highlight that 30% of the tested dogs avoided consumption of the meat experimentally smeared with vomit even as a second option. This result clearly shows that roller vomit can be effective in avoiding nestling predation".

APPENDIX 11A - PREDATOR-PREY INTERACTIONS

Predators follow a number of phases in getting prey:

i) Searching for prey generally - including finding sites where prey are or where they leave cues that they have been or will be.

ii) Detection of prey specifically - eg: echolocation of bats.

iii) Capture - eg: snakes use venom or constriction.

iv) Handle (ie: subdue and place in mouth) - eg: insects that grasp prey with legs and part in mouth.

In these phases of predation, spiders use multiple cues to find prey (especially chemical cues), their web to capture prey, and specific body structures to handle the prey, for instance (Segovia et al 2015).

But predator-prey interactions are an evolutionary "arms race" (Dawkins and Krebs 1979), where prey evolve defences to the predator's strategies, and the predators subsequently evolve counter-strategies to the new defence, and so on.

Different species of harvestman are prey for different spiders, and they have evolved defences, like mimicry, fleeing, chemicals, and thick skin that spiders cannot bite through. Willemart and Pellegetti-Franco (2006) found the latter defence to be effective as one species of harvestman (*Mischonyx cuspidatus*) survived for seventy days in a small terrarium with a predator spider

(*Enoploctenus cyclothorax*) who had no other food source.

The recluse spider (*Loxosceles gaucho*), however, has evolved a counter-strategy ("unique hunting strategy") to the "armour" of the harvestman (*Mischonyx cuspidatus*). Segovia et al (2015) studied the predator-prey interactions of these species captured in Brazil.

In the first experiment, the researchers investigated whether the recluse spider used chemical cues left by their prey to locate them. A spider was offered a choice of filter paper covered by chemicals from a harvestman vs no chemical, a cricket vs no chemical, or a cricket vs a harvestman. The spider was given thirty minutes to forage and the time spent on each filter paper was recorded. Nineteen spiders were tested. They showed no preference for filter paper, which suggested that chemical cues are not used in the search for prey.

However, the spiders were sensitive to chemical cues because they spent more time on the no-chemical filter paper. "Thus, these spiders apparently can detect chemicals on the substrate, but for some reason they do not use this information to select foraging sites" (Segovia et al 2015 p173).

The second experiment tested whether recluse spiders used vibrations to detect their prey. A harvestman or a cricket was placed on filter paper (which transmits vibrations) or on a granite surface (which does not). The success of prey capture was scored for fourteen spiders in each condition. The same number of prey were captured on both surfaces, which suggested that vibrations are not used in prey detection. The recluse spider may use other means of prey detection, like air displacement.

The third experiment investigated the handling of prey, and the use of webs to help to bite the vulnerable areas of the harvestman. In each case, a harvestman was placed in a terrarium with a spider with a web ($n = 19$) or with a spider where the web had been removed by the researchers ($n = 19$). The capture success was scored after one hour. There was no significant difference between the two conditions.

All three experiments were contrary to predictions. Yet the predation rates were higher than other more robust spiders in other studies. It seems that the recluse spider has evolved a strategy of touching the prey with its legs (ie: feeling for weak spots on the harvestman's body) before biting. This is more discriminate biting, which reduced the risk of damage to the mouth, compared to other spiders that bite prey indiscriminately. Discriminate biting is as effective with a web as not (and this explains the findings in

Experiment 3). Segovia et al (2015) stated that their research "demonstrates how a delicate predator can subdue a well-defended and heavy-bodied prey by handling it carefully, finding the weak spots and biting many times. Our results also clearly suggest the importance of tactile cues to find such weak spots. Taken together, our study shows the importance of avoiding generalisations when studying prey-predator interactions, since several of our results contrast with what would be expected based on previous studies of spider behaviour" (p175).

APPENDIX 11B - SOCIAL PARASITES AND CHEMICAL DISGUISE

Social parasites of insect colonies disguise themselves with chemicals similar to the host (ie: camouflage or mimicry), or by having "chemical insignificance". The former is done by rubbing against hosts, for example, while chemical insignificance involves having low concentrations of the chemicals. Such low levels mean the parasite is overlooked by colony defenders. Chemical mimicry evolves in social parasites that are linked to one host species, whereas chemical insignificance allows the parasitisation of more than one species (Nehring et al 2015).

There are social parasites that use both techniques. Slave-making ant queens (*Polyergus rufescens*), for instance, are chemically insignificant as they enter the host colony, but then come to mimic the chemical profile of the host queen (Lenoir et al 2001).

Nehring et al (2015) found a similar process among the social parasite queens of *Acromyrmex insinuator* in relation to its host, the leaf-cutting ant (*Acromyrmex echinator*) in Panama. Colonies were set up in the laboratory, and the researchers introduced a parasite queen or leaf-cutting ant queen into them. The reactions of worker ants for three minutes after introduction were observed. Both sets of queens were attacked equally, but parasite queens who survived subsequently received less aggression. The parasite queens remained calm during attacks whereas host queens fought back. The former, by this behaviour, "possibly appear less threatening and therefore host worker attacks might be less fierce or stop earlier" (Nehring et al 2015 p62). This fits with the idea of a "stealthy" parasite (Nehring et al 2015).

The cuticular chemical profiles of the queens were analysed. Initially, parasite queens showed chemical insignificance. This was "a perfect strategy for social parasites not to produce any substance that interferes with nestmate recognition, since ants appear to react to labels that do not match that of their colony, but not to individuals that lack parts of the colony-specific label" (Nehring et al 2015 p62). Subsequently, with

"every hour of close contact between parasite queens and host workers, cuticular substances will probably be transferred, leading to the cuticular profile of the parasites becoming more similar to that of the host colony" (Nehring et al 2015 p62).

APPENDIX 11C - SELF-SACRIFICING DEFENSIVE BEHAVIOUR

Self-sacrificing defensive behaviours can be divided into three types (Shorter and Rueppell 2012):

i) Instantaneous defence - Death of defender in engaging the enemy (eg: autothysis, sting autotomy).

ii) Pre-emptive defence - Self-sacrifice before a predator is encountered (eg: suicidal release of a substance in repairing a nest). Among *Forelius pusillus* (ant), a few workers remain outside the ground nest at night to conceal the entrance hole, and are unlikely to survive the night (Tofilski et al 2008).

iii) Altruistic self-removal (host suicide) - used against parasites.

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12. WHEN TO FIGHT?

12.1. DECIDING TO FIGHT

When two animals (usually males) compete over a resource (appendix 12A), fighting every time can be costly ⁷⁵, so the competitors assess their opponent to decide if withdrawing may be a better strategy than a costly losing fight. The fighting ability of a competitor is called their "resource-holding potential" (RHP) (Maynard Smith 1974).

A number of models based on game theory have been proposed to explain RHP by competitors based on self or mutual assessment, including (Schnell et al 2015):

i) Energetic war of attrition (E-WOA) (Payne and Pagel 1996) - The individual assesses their own RHP, but not their opponent's, and withdraws from the competition when the energy cost of continuing is too high.

ii) Cumulative assessment model (CAM) (Payne 1998) - Self-assessment of RHP, and withdrawal based on energy, time, and damage by opponent.

iii) Sequential assessment model (SAM) (Enquist and Leimar 1983) - The individual assesses the relative RHP of their opponent to themselves (mutual assessment), specifically RHP asymmetry (eg: one party is clearly larger than the other).

"Mutual assessment is assumed to be a more efficient strategy than self-assessment because animals can minimise costly and futile persistence by gathering information about relative RHP" (Schnell et al 2015 p32). But how do individuals make the mutual assessment of RHP? Schnell et al (2015) attempted to answer this question with a study of male giant Australian cuttlefish (*Sepia apama*).

Twenty-two individuals that varied in body size were randomly paired together in a contest arena. Larger individuals (ie: longer mantle length) were more likely to win in seventy-five observed contests. This established the key element of RHP.

Schnell et al (2015) summed up how the results fitted with the game theory models: "Winners and losers did not match behaviours during contests, ruling out the E-WOA model. There was no significant interaction between contest outcome, contest duration and the rates of

⁷⁵ "Escalated fights can be costly in terms of risk of injury, energy expenditure, exposure to predators and time dedicated to fighting that could be spent engaging in other activities" (O'Connor et al 2015 p19). Fatal fighting does occur though (appendix 12B).

escalation, which violates the assumption of the CAM. Persistence to continue a fight was based on RHP asymmetry, rather than loser and/or winner RHP, indicating that the SAM is the most likely candidate model" (p37).

The males were "able to modify their behaviour as a function of the realised state of their opponent relative to their own, indicating that they use mutual assessment to resolve male-male contests" (Schnell et al 2015 p37).

Individuals will bear higher costs for more valuable resources (objective resource value), and depending on their motivation (subjective resource value). For example, food-deprived individuals may fight more vigorously for food than well-fed individuals (O'Connor et al 2015). While male house crickets who have not mated recently (ie: female deprived) are more aggressive and win more fights over females than males who have not been deprived of females (Brown et al 2007).

Territorial residents have an advantage over intruders/challengers either because of greater motivation to win, being in a better condition, or "ownership convention" (ie: "where the ownership of a territory is an arbitrary means to settle disputes between well-matched individuals, while avoiding costly confrontations"; O'Conner et al 2015).

O'Connor et al (2015) felt that contests staged in laboratory experiments "may not reflect the full range of motivational effects that influence decision making in wild animals". So, they studied the male daffodil cichlid fish (*Neolamprologus pulcher*) in its natural habitat (with a field experiment).

The following predictions were tested:

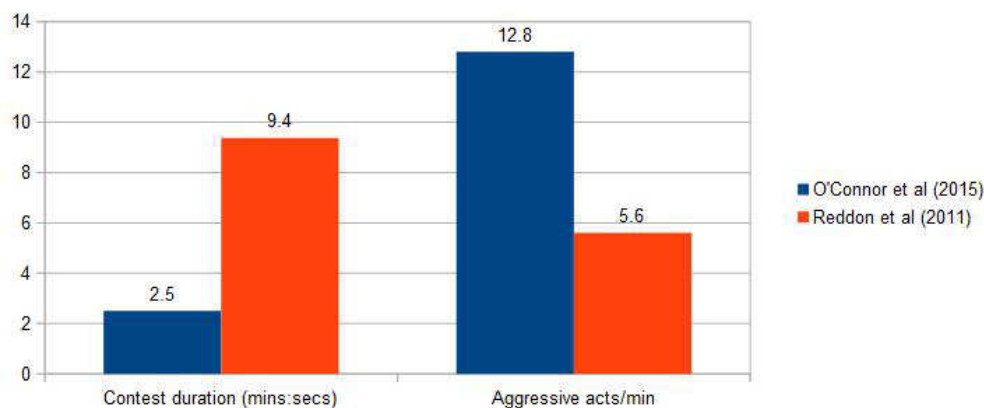
1. Larger individuals will win more often than smaller individuals.
2. Individuals will be more willing to incur higher costs for more valuable resources (eg: access to many females rather than an individual female).
3. Individuals with greater motivation will fight harder (eg: single territory versus multiple territories).

Contests between males were staged by removing the resident male from his territory for a short period (eg: four hours) or a long period (eg: twenty hours). The original resident was returned and a territorial contest with a usurper resident occurred on twenty-one short removal and eleven long removal trials. Aggressive behaviour was scored as displays (eg: aggressive postures) and overt attacks (eg: bites). The trials took

place in Kasakalawe Bay in Lake Tanganyika, Zambia in early 2013.

The first prediction about body size was not supported by the data, nor the second prediction. But individuals with a single territory (ie: subjective resource value) displayed higher rates of aggression (third prediction).

The contests were significantly different to laboratory staged contests (Reddon et al 2011) - eg: shorter and more intense (figure 12.1).



(Data from O'Connor et al 2015 table 1 p23)

Figure 12.1 - Significant differences between contests in O'Connor et al (2015) and Reddon et al (2011).

12.2. AVOIDING CONFLICT

Males may not always try to mate as much as possible. In species where large body size wins male-male contests, it makes sense to spend time and resources on growing (where growth continues past maturation) than trying to compete for mates.

This is so with a hermit crab (*Pagurus filholi*). Males use pre-copulatory guarding of females, where they grasp the gastropod shell occupied by a mature female for several days until she is ready to mate. The grasping of the shell means no feeding opportunity, and the likelihood of male-male conflict if a solitary male arrives.

Hasaba et al (2015) used hermit crabs caught in low tides near Hokkaido, Japan in their experiments. In one condition, a female and a guard male along with a solitary male were placed together to create male-male conflict, and a male was offered two females to choose to guard in another condition.

Non-guarding males were found to be more likely to

moult within five days after the experiment than guarding males. This fitted with the "concept of optimal allocation between present and future reproduction... [as] small males of *P. filholi* show a lower frequency of guarding to allocate more energy and time for growth. During the long mating season of 8 months, males of *P. filholi* may not maximise resource allocation to the present potential mate but allocate them to growth, consequently increasing future mating success" (Hasaba et al 2015 p4).

12.3. KIN DISCRIMINATION

Discriminating kin from non-kin (and familiar from unfamiliar neighbours) is important in knowing who is a territorial threat or not. There are different ways to discrimination (Wilson et al 2015):

a) Location-based - In species that live in kin groups close together, individuals nearby are assumed to be kin.

b) Familiarity-based - Learning to recognise certain individuals from repeated interactions.

c) "Phenotype matching" - A generalised template to recognise unfamiliar kin based on traits of the self or mother, say.

d) "Recognition alleles" - Kin share a particular trait which is the means of recognition.

Mateo (2003) reported the use of familiarity-based discrimination and phenotype matching among rodents, usually based on smell.

Applying these ideas to territorial disputes, North American red squirrels (*Tamiasciurus hudsonicus*) (figure 12.2) avoid fights usually by the use of territorial vocalisations called "rattles" (a series of pulses in rapid succession) (Wilson et al 2015).

Price et al (1990) found that squirrels could distinguish the rattles of neighbours and non-neighbours in a playback experiment. "However, because neighbours tend to have greater relatedness than non-neighbours..., it is unclear whether squirrels in that study were discriminating between neighbours and non-neighbours, kin and non-kin, or both..." (Wilson et al 2015 p80).

Wilson et al (2015) tested red squirrels in south-west Yukon, Canada, in a similar playback experiment, but it compared the rattles of neighbouring kin, neighbouring non-kin, non-neighbouring kin, and non-neighbouring non-kin. It was predicted that the territory owners would



(Source: D.Gordon.E.Robertson; <https://commons.wikimedia.org/wiki/User:Dger>)

Figure 12.2 - Red squirrel.

respond more aggressively to the rattles of (i) non-neighbours than neighbours, and (ii) non-kin than kin.

Territorial rattles were recorded from 172 squirrels in a marked population between 2005 and 2011. In the playback experiment, aggression was defined as a response rattle and movement towards the stereo speaker by the territory owner within three minutes of the playback.

Fifty-three adult squirrels were used in the field experiment, and in the control condition (no sound) eleven individuals showed aggression. The first hypothesis was not supported by the data - 37% of territory owners responded to neighbours' rattles and 50% to non-neighbours (but this difference was not significant). However, the second hypothesis was significantly different - 59% of squirrels responded to non-kin versus 25% to kin.

Wilson et al (2015) summed up: "Our playback study provided no evidence that red squirrels discriminate between the territorial rattles of neighbours and non-neighbours, despite the potential benefits that such discrimination could afford... We note that, among unrelated squirrels, neighbour status and familiarity are probably highly concordant. Thus, it is unclear whether

subjects failed to respond to differences in neighbour status or to differences in familiarity, although we are unaware of any biologically meaningful distinction between these in this species. Our findings contrast with a previous playback experiment [Price et al 1990], which found that squirrels were more likely to respond to rattles from non-neighbouring individuals" (p84).

The researchers linked their findings to the mechanisms of discrimination: "The often-prolonged proximity among mothers and offspring suggests that a familiarity-based mechanism could facilitate kin discrimination among these family members.... Note, however, that male red squirrels provide no paternal care and interact with their mates only during copulation.... Consequently, a familiarity-based mechanism would not allow red squirrels to discriminate between their fathers (and paternally related kin such as paternal half-sibs) and unrelated individuals" (Wilson et al 2015 p84).

12.4. MENTALISING IN COMPETITION

A complete assessment of a competitor would involve "mentalising" or "a theory of mind" (Premack and Woodruff 1978) (ie: "the ability to ascribe unobservable mental states to oneself and others"; Karg et al 2015). There is much debate as to whether this ability is uniquely human.

Povinelli and Vonk (2003) developed the "goggles experiment" design to study mentalising in non-human primates. There are two pairs of goggles, each with a different coloured frame. One pair is transparent (ie: the wearer can see through them) and the other is opaque (ie: the wearer cannot see anything). The participant, a chimpanzee, say, wears each pair of goggles for a while to build up self-experience. Then they are presented with two humans with food, each wearing a different pair of goggles. Who will the chimpanzee beg food from? "If primates are able to mentalise, they should use their own mental experience to infer the others' mental states, and prefer begging from the experimenter who wears the see-through goggles" (Karg et al 2015 p211).

Vonk and Povinelli (2011) found no difference in the human approached by chimpanzees, when using buckets on the head (see-through or opaque) rather than goggles.

Karg et al (2015) used a see-through and an opaque mask with chimpanzees (*Pan troglodytes*) at a sanctuary in Uganda. In their Experiment 1, twenty-five chimpanzees had eight minutes of self-experience with each mask in the experience phase. Then, in the test phase, the experiments measured whether the chimpanzees followed the gaze of the human just as they put on a mask. There was

no difference in looking in the correct direction by the chimpanzees based on the mask worn by the human. The researchers stated: "We conclude that there is no evidence that chimpanzees in this study used their own visual experience to infer what another can see" (Karg et al 2015 p214).

In Experiment 2, Karg et al (2015) used a competitive game with nineteen chimpanzees. The chimpanzees were trained on an apparatus that two different coloured boxes for food, one with a transparent lid and the other opaque. In the test phase, a human sat opposite the chimpanzee and the two boxes. When the animal reached into the transparent box, the human pulled it away (ie: because the human could see the chimpanzee's hand), but not when it was the opaque box (ie: successful stealing of food). There were three conditions:

1. Transparent - One lid was transparent and the other opaque.

2. Screen - The same two boxes were shown to the chimpanzee, but then a screen was placed on top so that both boxes appeared opaque to the animal (but not to the experimenter).

3. Control - As condition 1 but with no humans present.

The chimpanzees chose the opaque box significantly more often in the screen and transparent conditions than in the control condition, and the choice was significantly greater than chance. So, the "results demonstrate that chimpanzees were able to use their own experience with the visual properties of the lids to later infer in which box their approaching hand would be hidden from the experimenter" (Karg et al 2015 p218).

Karg et al (2015) dealt with potential criticisms that the chimpanzees were not using their self-experience, particularly in Experiment 2, to allow mentalising, but that there was a "lower-level" explanation for the findings.

- i) The experimenter gave behavioural cues as to which box to choose in Experiment 2. Karg et al (2015) replied that "the experimenter's body was oriented to the centre between the boxes and her gaze direction was not visible to the subject as she looked down towards the box lids" (p218).

- ii) The chimpanzees learned about the lids from observing the human's behaviour in Experiment 2. Karg et al's (2015) defence was that the "experimenter treated all lid types in the same way. In addition, the lids were

positioned such that the chimpanzee could never see the experimenter's eyes through the transparent lid or the screen" (p218).

iii) The chimpanzees learned to associate the colour of the opaque box with success in Experiment 2. This was not so because in the control condition the chimpanzees showed no preference for opaque or transparent box, choosing each about 50% of the time.

iv) The chimpanzees, who were semi-free ranging, could have observed other individuals in their natural environment and learned to choose the opaque box this way. Karg et al (2015) countered: "For this objection to apply to our experiment, chimpanzees would need to have experienced others looking through screens and then act as if they could see; it is unlikely that our subjects were ever exposed to such experiences as they live in a natural forest during the day and have no previous experience with experiments involving screens or others interacting with them" (p218).

v) The "evil eye hypothesis" (Povinelli and Vonk 2004). This is the idea that in "their everyday environment, subjects could have learnt rules about the contingencies of the eyes of a competitor and contested food, for example by imagining a line of sight between the competitor's eyes and the food" (Karg et al 2105 p218). As stated earlier, the human's gaze was not visible to the chimpanzees in Experiment 2.

vi) The chimpanzees "could have learnt about the 'psychological affordances' of the masks, such as 'able to be seen through' and 'unable to be seen through', instead of projecting their visual experience to the competitor" (Karg et al 2015 p219). The researchers argued that even if this was the case, this was evidence of mental representation of an object that is different to their own viewpoint, which is a form of perspective-taking (or mentalising).

vii) Some researchers do not accept that non-human primates can mentalise. For example, Csibra (1998) stated: "Seeing is a mental concept if, and only if, it refers to an epistemic relation between a mind and an object/ event that is established in a particular (visual) way; but it is not a mental concept when it refers only to the physical relations that may or may not give rise to the epistemic relation. Accordingly, demonstrating that animals can understand such a physical relation and can use it as a discriminatory cue to predict the usability of people's behaviour is not sufficient evidence for applying mental concepts. What is needed in addition is to demonstrate that the animals

conceive the result of seeing as a representational rather than a dispositional state" (quoted in Karg et al 2015 p219).

There are many other studies showing that chimpanzees understand what others see, hear, or know (Karg et al 2015).

viii) Challenges to the validity of the "goggles experiment" design with primates. Karg et al's (2015) research was based on a design used with 18-month old humans.

ix) Why did the chimpanzees behave differently in Experiments 1 and 2? Primarily, Karg et al (2015) said, because Experiment 2 was a competitive situation which is more familiar to chimpanzees. But also Experiment 2 have no time limits whereas a quick decision to follow the human's gaze was required in Experiment 1.

Furthermore, Karg et al (2015) admitted: "while subjects could use only the frame colour as a cue to the visual properties of the mask in experiment 1, they could use frame colour and/or location of the lid (left/right of the experimenter) as a cue in the second study. Obviously, the location of the rewarded lid varied randomly between the trials; however, in the experience phase of each trial, they could learn not only about the frame colour, but also about the location of the (truly) opaque lid. Several studies have demonstrated that chimpanzees have difficulties with quickly associating arbitrary cues such as colour with the presence of food..., which might account for their indiscriminate gaze-following behaviour in experiment 1. Other studies show that chimpanzees prefer location to colour as a cue to find food" (pp219-220).

APPENDIX 12A - NEIGHBOURS COMPETING

Neighbours compete in two ways (Sorvari and Hakkarainen 2004):

- Directly - "interference competition" (fighting between individuals for resources).
- Indirectly - "exploitation competition" (resources used by one individual deprives another).

On the other hand, neighbours may co-exist without competing, especially if food resources are abundant and stable. This is known as polydomy, as in the case of colonies of ants. However, this may change if the food resources become scarce (Sorvari and Hakkarainen 2004).

Sorvari and Hakkarainen (2004) showed this change among colonies of wood ants (*Formica aquilonia*) in a field study in 2002 in central Finland where trees had

been cut down (clear-cut). Eleven areas deforested in the late 1990s were compared to fourteen areas still forested (controls). The ant collect seeds, arthropods, or aphid excretions as their food source.

Ten worker ants from each of two neighbouring colonies were put in an arena and the number of ants fighting one minute after the test started was scored. Each colony was tested against three of its neighbours.

There were significantly more fights between ants from clear-cut neighbouring colonies than between controls. Sorvari and Hakkarainen (2004) explained the findings thus: "We suggest two reasons for the increased aggressive behaviour in clear-cuts. First, clear-cuts may decrease food resource levels by reducing the number of trees providing aphids... This may induce competition for the diminished food resources. Second, wood ants use landmarks, such as trees, as visual orientation cues... Disappearance of trees may collapse the route system between formerly co-operative neighbouring colonies... Therefore, the alienation of neighbouring colonies and decreased food resources may give rise to competition in clear-cuts" (p152).

The researchers highlighted the harmful effect of human disturbances to the forest/environment.

APPENDIX 12B - FATAL FIGHTING

Fatal fighting does occur sometimes, and the risk of death must be outweighed by the benefits of winning in a species (Enquist and Leimar 1990). In the case of ants, for example, the death of sterile workers to defend the colony benefits their related reproductive adults.

"Large-scale battles are most likely when the future of the nest is at stake, since all members of the colony stand to lose their genetic contribution to the next generation if the nest is lost" (Cunningham et al 2014 p777).

Colonies of an Australian stingless bee (Sugarbag bee) (*Tetragonula carbonaria*) fight each other (intraspecies warfare) and other closely-related stingless bees (*Tetragonula hockingsi*) (interspecies warfare) (Goldman 2015).

Cunningham et al (2014) studied the fights of a colony of Sugarbag bees in a man-made nest box in Brisbane, Australia, in 2008, using the bodies of dead bees in genetic analysis. Data were also collected on 260 hives across south-east Queensland between 2008 and 2012.

There was evidence of interspecific warfare, with the benefit of a fully provisioned nest for the winners, and mating opportunity. The new queens were found to be daughters of attacking hive's own queen. Goldman (2015) observed: "When the reproductive capacity of the royal

class is at stake, the potential benefits of either colony may outweigh the risks of massive casualties".

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13. BIRDS AND THINKING ABOUT THE FUTURE

13.1. CACHING BEHAVIOUR

The ability to think about the future is seen in long-term food storage by species that do not have a continuous supply of food available. But caching behaviour could be instinctive (eg: triggered by hormones in autumn).

However, scatter-hoarding suggests cognitive abilities beyond mere "automatic" behaviour. Such animals, like squirrels and some birds, do not cache their food randomly in their territories, but choose sites with specific environmental characteristics (Neuschulz et al 2015).

One explanation for scatter hoarding is to reduce pilferage by own and other species. For example, squirrels cache their most valuable food away from their favourite trees, with increased predation risk when retrieving, but where the risk of pilferage is lower (Steele et al 2014).

Perishability of food may also influence the caching strategy. Seeds that take longer to germinate (ie: less perishable) are cached, while those near to ripening are eaten immediately or sooner. The rate of germination is affected by the environment where the seed is stored. Seeds are more likely to establish themselves in areas of sunlight and moist soil.

Neuschulz et al (2015) found that spotted nutcrackers (*Nucifraga caryocatactes*), in the Swiss Alps, showed awareness of the environment when caching seeds of Swiss stone pine. Between mid-August and October 2012, nearly four hundred hours of observations were made of these birds. The researchers calculated the canopy openness (ie: amount of sunlight) and soil moisture at sites where birds were seen to cache the seeds.

Caching was most common in sites with high tree cover (canopy openness less than 5%) and dry conditions (soil moisture less than 5%), while sites with intermediate soil moisture (45-55%) and no tree cover were least common. This suggested that "nutcrackers may follow a strategy to prevent seed perishability by caching seeds at sites that are unfavourable for pine establishment" (Neuschulz et al 2015 p75). Goldman (2015) put it this way: "The spotted nutcrackers have learned to use nature as a breadbox, keeping their food from spoiling".

Pilferage was not affected by the environment where the seed cached, which suggested that this is less important in the caching strategy.

Caching behaviour is effective generally because of the excellent spatial memory of the nutcracker (eg: 80%

of caches found; Mattes 1982 quoted in Neuschulz et al 2015).

13.2. META-COGNITION

"When humans mentally reconstruct past events and imagine future scenarios, their subjective experience of mentally time travelling is accompanied by the awareness of doing so" (Watanabe et al 2014 p859). This awareness is meta-cognition. With humans it can be tested by asking how confident an individual is about their recall of information to a question. But how to study meta-cognition among non-human animals?

One method is to give the animals the choice to seek more information. For example, an animal is trained on a delayed matching-to-sample task with a food reward. This involves showing a stimulus (eg: round shape) and then a short while later a choice (matching task) involving the seen stimulus and a new one (eg: square shape). Correct choice of the seen stimulus gives the food reward. This is a basic memory and learning task. Meta-cognition is tested by offering a trained animal the choice of the stimulus before the matching task or going directly to the matching task. Meta-cognition would involve knowing that the stimulus needs to be seen before the matching task. Pigeons tested in this way go straight to the matching task, whereas rhesus macaques and capuchin monkeys choose to see the stimulus (Watanabe et al 2014).

Watanabe et al (2014) designed an experiment related to caching and pilferage with Western scrub-jays (*Aphelocoma californica*). In the wild, these birds watch conspecifics hiding food and then steal it, but also hide food knowing that they are being watched and recached it when not observed.

In the experiment, five birds had a choice of two experimenters to watch for thirty seconds. In the free-choice compartment, the experimenter hides food in one of four open cups, while in the forced-choice compartment, food is hidden in an open cup with three others having closed lids. It was set up so that the birds gained no additional information about the location of food by watching the forced-choice compartment, and evidence of meta-cognition would be seen in less time watching this experimenter.

The birds spent significantly more time looking at the free-choice compartment (mean: 14 seconds) than the forced-choice compartment (mean: 10 seconds), and made significantly more looks (3 vs 2). Watanabe et al (2014) summed up: "When given the choice, we found that the jays looked for longer, and more frequently, into the compartment they were trained to recognise as the one in which they will use the information gained regarding the

location of food being baited [free-choice compartment], while paying less attention to the compartment where information was not important [forced-choice compartment]" (p865).

The researchers admitted: "It should be noted that we did not address the question of whether the birds are fully aware that they are using the above study strategy. In the absence of agreed behavioural markers of phenomenological consciousness, this is not possible in non-linguistic animals. But what our experiment may provide is a basis for establishing the behavioural criteria of meta-cognition in such animals..." (Watanabe et al 2015 p866). Friederike Hillemann described the experiment as "an elegant way to determine whether animals are capable of reasoning about their own knowledge states" (quoted in Goldman 2014).

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14. CAMOUFLAGE - HIDING IN PLAIN SIGHT: TWO EXAMPLES

14.1. TAWNY FROGMOUTH

The roosts (and nest sites) of birds need to provide protection or camouflage from predators, and to aid temperature regulation, particularly in cold climates (Kortner and Geiser 1999).

Nocturnal birds that rest during the daytime particularly need camouflage, like the tawny frogmouth (*Podargus strigoides*) in Australia.

This bird has a cryptic plumage, which along with its posture, means it resembles a broken branch (Kortner and Geiser 1999) (figure 14.1).



(Source: C Coverdale; copyright free)

Figure 14.1 - Tawny frogmouths.

During their observations in Eastwood state forest in north New South Wales, Australia, in 1997-8, Kortner and Geiser (1999) reported that frogmouths "assumed a typically out-stretched branch-like posture which presumably decreases the likelihood of being detected" when large birds (predators) were nearby. Also frogmouths

tend not to fly during the day and so their camouflage is not jeopardised by movement.

Kortner and Geiser (1999) summed up their observations: "Tawny frogmouths preferred stringybarks presumably because the rough bark is so similar in appearance to the bird's mottled plumage. If a gum was chosen as day roost, then dead grey-coloured branches blending with the plumage of the resting bird were frequently selected as roosts. To conceal the bulk of the body further, frogmouths either roosted along medium sized branches or in a fork. Particularly when sitting on a thin branch, frogmouths tended to press their body against the trunk or another larger branch. Camouflage thus appears to be an important criterion for roost selection by frogmouths" (p506).

This compares to the less cryptic/camouflaged owlet-nightjar (*Aegotheles cristatus*) in the same area which roosts in tree hollows to avoid predators (Kortner and Geiser 1999).

14.2. SLENDER FILEFISH

Slender filefish (*Monacanthus tomentosus*) (figure 14.2) change their colouration to create "false edges", and thus make them "invisible" against the background. Objects are perceived by distinguishing the edges. For example, the filefish makes a dark, longitudinal stripe appear on its body which looks like a real edge, and the viewer misses the true outline of the fish (In Brief 2015).

The fish also has skin (dermal) flaps that protrude, and make the physical edges appear less smooth (and like small clumps of sand), and again confuse predators (In Brief 2015).

Allen et al (2015) filmed filefish on the reefs of Bloody Bay, Little Cayman (Cayman Islands) between April 2009 and June 2012. Forty-six body pattern changes were recorded, and the speed of change varied from one to thirteen seconds. The coral reef is inhabited by predators with powerful vision, and the ability to change body pattern allows the slender filefish to forage stealthily.

Overall, Allen et al (2015) highlighted five ways the filefish were avoiding visual detection:

- Colour resemblance to background.
- Scale resemblance to background.
- Disguising the body's edges with dermal flaps.
- Moving its body in rhythm with the coral branches.
- By "maintaining a head-down body orientation that is similar to the main axes of the background elements" (p390).



(Source: Nhobgood)

Figure 14.2 - Slender filefish.

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15. INBREEDING AVOIDANCE IN TWO INSECTS: YES AND NO

"Inbreeding depression" refers to the negative effects of inbreeding, like increased risk of recessive gene conditions, and reduced variation among offspring. This has led to the evolution of inbreeding avoidance strategies (Blouin and Blouin 1988), usually based on dispersal and/or kin recognition.

Fischer et al (2015) described the importance of inbreeding avoidance among females of a solitary tropical butterfly - the squinting bush brown (*Bicyclus anynana*) (figure 15.1) that was very sensitive to inbreeding depression. In 212 mating trials, where virgin females were offered a brother or an unrelated male, the latter had significantly more matings. This difference was more pronounced in an inbred generation (previously kin mated) than an outbred generation.



(Source: Gilles San Martin)

Figure 15.1 - Squinting bush brown.

Kokko and Ots (2006) predicted that inbreeding avoidance is more likely when mate choice is simultaneous (ie: multiple mates available at same time) than sequential (ie: multiple partners available one by one). Matthey and Smiseth (2015) pointed out that "females can

make a direct comparison between related and unrelated mates when they encounter males simultaneously, while females must make a decision about whether or not to mate with a single male based on a template of a preferred partner when they encounter males sequentially" (p1036).

Mattey and Smiseth (2015) found no support for this prediction among females of a burying beetle (common Sexton beetle) (*Nicrophorus vespilloides*) (figure 15.2). In the wild, simultaneous mating occurs when many males and females gather on a carcass, while sequential mating opportunities arise when there is no carcass.



(Source: Calk Eklund/V-wolf)

Figure - Two common Sexton beetles on rat carcass.

The researchers created the two mating scenarios in the laboratory offering a female the choice of a full sibling or an unrelated male together in the presence of a rat carcass or sequentially without the carcass. There was no difference in mate choice in 26 simultaneous trials and 41 sequential trials. This finding is contrary to expectation as this beetle suffers from severe inbreeding depression (eg: inbred individuals have less survival to adulthood).

There are a number of possible reasons for no inbreeding avoidance (Mattey and Smiseth 2015):

i) High opportunity costs of mating - ie: it is better to mate than not irrelevant of partner's relatedness.

ii) No kin recognition mechanism.

iii) Few costs to inbreeding.

iv) Low risk of inbreeding - ie: meeting kin is rare.

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16. SEX DETERMINED BY CHROMOSOME OR ENVIRONMENT?

The determination of sex of offspring occurs by heterogamety (eg: presence of XX or XY chromosomes) or the temperature of the nest during egg development (eg: reptiles) ⁷⁶. The former is a genotype mode of sex determination and the latter is environmental. But these modes are "not mutually exclusive dichotomous strategies" (Holleley et al 2015).

One example of both modes at work is the Australian central bearded dragon (*Pogona vitticeps*) (figure 16.1). There is a heterogametic system where ZZ chromosomes produce male (ZZm) and ZW female (ZWf), but high incubation temperatures can lead to males becoming females (ZZf) (Holleley et al 2015).



(Source: Karelj; in public domain)

Figure 16.1 - Central bearded dragon in a zoo.

Holleley et al (2015) sampled the wild population of these lizards near the border between Queensland and New South Wales over a number of years finding that sex-reversed females (ZZf) were between 7-22% of the sample,

⁷⁶ In a recent study of human sperm, it was found that the ratio of Y- to X-bearing chromosomes declines with age (Stone et al 2013). The upshot is that older men are likely to father more daughters.

and they laid significantly more eggs per year than ZW females.

The researchers then incubated eggs at different temperatures. Between 22 and 32°C sex was determined by chromosomes, but above 32°C the environment became dominant. At 36°C almost all offspring hatched were ZZf. But ZZf's own eggs were subsequently found to be more sensitive to temperature, and sex-reversed females appeared at a lower temperature.

This study showed that the "experimental transition from genotypic sex determination (GSD) to TSD [temperature sex determination] demonstrates a novel transitional pathway, in which TSD can evolve rapidly in response to extreme environmental conditions (high temperatures) without requiring that there be sex-specific selective advantages" (Holleley et al 2015 p81).

The W chromosome is eliminated, and this may be a clue to the effect of warming climate. Holleley et al (2015) warned: "Exposure to high temperatures can perturb apparently stable GSD systems, induce a rapid transition to TSD and then proceed inexorably towards a highly feminised population and thus a greater risk of extinction" (p81).

Bull (2015) summarised the two key issues with GSD and TSD together:

i) If ZW males and ZW females mated subsequently, they could have offspring with WW chromosomes, which would be inviable or sterile. This is overcome by the fact that ZW is always female.

ii) The high temperature at incubation produces only females. This is overcome by "sex-ratio selection, which automatically adjusts the frequency of the W chromosome to progressively lower levels as more ZZ females are produced" (Bull 2015 p44).

Ohno (1967) had argued that "an inexorable evolutionary progression from genetically labile mechanism of sex determination to highly refined and differentiated sex chromosomes" (Bull 2015 p43). So fish had TSD, mammals and birds GSD, and reptiles "in the middle of the transition" (Bull 2015). Janzen and Paukstis (1991) showed that this view was too simplistic - "the evolution of sex determination follows basic evolutionary principles, and that chromosomal and environmental sex determination can both be highly functional, adaptive systems. In other words, they are not different steps along an evolutionary progression, but are alternative states that could, in theory, evolve back and forth" (Bull 2015 pp43-44). But it was assumed that each reptile species had one mode or the other. The

work by Holleley et al (2015) challenged this view ⁷⁷.

APPENDIX 16A - RECENT IDEAS ABOUT EVOLUTIONARY THEORY

Evolution is assumed to follow the path of mutate first and adapt later, but there is evidence that "animals often adapt first and mutate later" (Barras 2015) ⁷⁸. The idea that the behaviour or characteristics acquired in an individual's lifetime can be passed onto the next generation genetically was proposed by Jean-Baptiste Lamarck in the late eighteenth and early nineteenth centuries. But the dominant thinking on evolution today is that there is "no way for information about what animals do during their lifetime to be passed on to their offspring" (Barras 2015).

In the mid-20th century, Conrad Hal Waddington coined the term "genetic assimilation" (eg: Waddington 1961). "The acquired characteristics don't shape the genetic changes directly as Darwin proposed, they merely allow animals to thrive in environments that favour certain mutations when they occur by chance" (Barras 2015 p29).

Growth in knowledge about genes, and ideas like epigenetics ⁷⁹ have produced a "growing appreciation of the flexibility of genes" (Barras 2015). Genes are not rigidly preprogramming, but the environment can have an influence on their expression. The debate about genetic assimilation continues ^{80 81}.

⁷⁷ Challenges to traditional views and contested ideas are common in science, including in relation to evolutionary theory (appendix 16A).

⁷⁸ von Bertalanffy (1952) noted that "the changes undergone by organisms in the course of evolution do not appear to be completely fortuitous and accidental; rather they are restricted, first by the variations possible in the genes, secondly, by those possible in development, that is, in the action of the genic system, thirdly, by general laws of organisation" (quoted in Drack 2015 p84).

⁷⁹ "Pollutants, stress, diet and other environmental factors can cause persistent changes in the mix of epigenetic marks in chromosomes and, in that way, can alter how cells and tissue behave. Surprisingly, some acquired changes can be passed on to descendants" (Skinner 2014 p36).

Skinner (2014) outlined the implications: "If the environment can sometimes directly produce long-term, transgenerational changes in gene activity without first altering the DNA coding sequence, then the classical view of evolution - as a slow product of random mutations that get 'selected' because of the reproductive or survival advantage they offer - will have to be expanded... Epigenetic changes appear to occur 1000 times more frequently. The most important effect of epigenetic marks - maybe their reason for existing - might be to wildly expand the number of variant individuals in a population. Natural selection would then pick the best adapted among them to thrive and carry on - genome, epigenome, and all" (p41).

⁸⁰ Elsdon-Baker (2009) observed: "Take heredity... you might think that the case has long been closed on how it works. In fact, there are competing perspectives stretching back over 150 years. Darwin himself was a pluralist and proposed a theory of heredity that allowed not only for the inheritance of latent characteristics but also for the environment to play a role in it" (p24).

⁸¹ The term "biomogenesis" has been used to describe "evolution as the result of complex causal relationships of the environment as well as in the organism itself" (Drack 2015 p86).

An interesting study by Standen et al (2014) has shown adaptation over the lifetime. Bichir fishes (figure 16.2), that can breathe air and haul themselves over land, were kept from a young age in an aquarium with little water. Over a period of eight months their skeletons changed to aid movement on land (Barras 2015).

Critics say that these changes would need to be fixed by mutations that could be passed onto the next generation (Barras 2015). Also it has not been shown that the physical changes in the bichir fish continue in their offspring (Barras 2015).

Studies like this are showing developmental plasticity (ie: physical changes in the lifetime of the individual), but whether they are passed onto the next generation is contested.



(Source: Mitternacht90; in public domain)

Figure 16.2 - Senegal bichir.

Complexity

The variety of ideas about evolution can be seen

with neutral evolution (Kimura 1984)⁸² and "constructive neutral evolution" (Gray et al 2010). Zimmer (2013) summed up: "Conventional wisdom holds that complex structures evolve from simpler ones, step-by-step, through a gradual evolutionary process, with Darwinian selection favouring intermediate forms along the way. But... complexity can arise by other means - as a side effect, for instance - even without natural selection to promote it... [;] random mutations that individually have no effect on an organism can fuel the emergence of complexity..." (p78).

Similarly, McShea and Brandon (2010) referred to the "zero-force evolutionary law" - ie: complexity increases even in the absence of natural selection. For example, comparing fruit flies bred and raised in laboratories to those in the wild, the former have experienced less pressure to eliminate disadvantageous mutations and have become more complex (Fleming and McShea 2013).

Douglas Erwin was not convinced. According to the "zero-force evolutionary theory" "complexity may increase in the absence of selection. But that would be true only if organisms could actually exist beyond the influence of selection. In the real world, even when they are pampered by the most dotting of scientists... selection still exerts a force" (on fruit flies) (quoted in Zimmer 2013).

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⁸² Neutral theory of evolution sees that genetic mutations persist in the population that are selectively neutral (ie: no positive or negative appreciable effect on fitness). But this theory underestimates the importance of natural selection (Orr 2009).

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