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Animal Parenting

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

A complete listing of his writings at http://kmbpsychology.jottit.com and http://psychologywritings.synthasite.com/.

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1. MOTHERS, FATHERS, AND ANIMAL PARENTS

1.1. NO FATHERS

Parthenogenesis is where, among animals that reproduce sexually, an egg develops without being fertilised by a sperm (a "virgin birth"). Generally, it was believed to be rare (eg: females alone in captivity), but more cases are being found in the wild (eg: boa constrictors, pit vipers, turkeys), even when plenty of males are available (Pilcher 2013).

Parthenogenesis allows a species to grow faster as animals can spend more time looking for food rather than mates, and the dangers of mating are removed (eg: disease or injury by male). A new combination of genes from sexual reproduction may not be any better than the current set (Pilcher 2013).

On the downside, all-female species produced by parthenogenesis are likely to go extinct after 10 000 - 100 000 generations (Pilcher 2013). No sexual reproduction means no shuffling of genes, and harmful mutations have an effect on survival of the species [1]. The offspring of parthenogenesis are severely inbred, and their survival is limited. For example, a captive female zebra shark in the Burj Al Arab aquarium in Dubai produced over a hundred eggs over several years with only four surviving (Pilcher 2013).

There is another situation where egg development needs the stimulation of sperm, but the offspring inherit 100% of the mother's genes. This is known as gynogenesis. This was first observed in 1932 in a fish called the Amazon molly (Poecilia formosa) (figure 1.1), which is all-female. They mate with males of related species (Pilcher 2013).

One species, the Ambystoma mole salamander, for example, occasionally keeps some of the DNA from mating with males of another species (to stimulate egg development). This is known as kleptogenesis (Bogart et al 2007).

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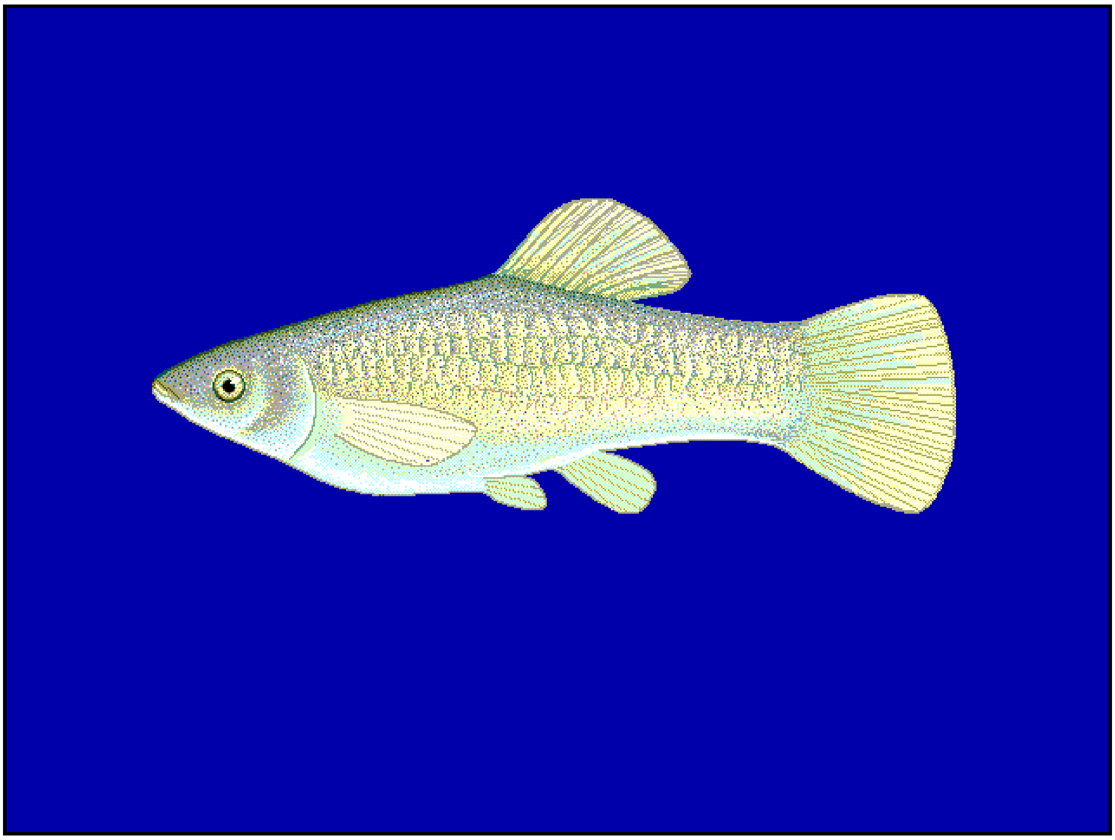
[1] Because the offspring are clones of the mother, they will carry the same detrimental mutations, and, as in asexual populations generally, this will produce lower evolutionary fitness. This has been called the "mutational ratchet" (Muller 1964) or "mutational melt-down" (Lynch and Gabriel 1990).



(Source: Robbie N Cada; in public domain)

Figure 1.1 - Drawing of Amazon molly.

How does a female unisexual species evolve? [2] It seems that it is a product of a mating between two similar species. For example, the unisexual New Mexico whiptail lizard (Aspidoscelis neomexicana) is the product of the mating between a male little striped whiptail (Aspidoscelis inornata) and a female western whiptail (Aspidoscelis tigris) (figure 1.2) (Pilcher 2013) [3].

This is less of an issue where virgin births can be both males and females. In birds and some reptiles, females have both male and female sex chromosomes (Pilcher 2013).

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[2] Another behaviour that is a challenge to evolution is female sexual cannibalism (appendix 1A).

[3] Lutes et al (2011) provided a "proof of principle" with a laboratory study that bred a male little striped whiptail lizard with a female Chihuahuan spotted whiptail lizard (Aspidoscelis exsanguis). The offspring were similar to the mother, but had differences that could be seen as a new species (ie: novel genotype).

(Source: Alistair J Cullum)

Figure 1.2 - 3 species of whiptail lizard - little striped (left), New Mexico (centre), and western (right).

1.1.1. Paternal Recognition

Kassler et al (2012) reported that female grey mouse lemur (Microcebus murinus) (figure 1.3) can recognise the calls of their father despite being raised by maternal kin only (mother and aunts). The father remains in the vicinity for years, and inbreeding is a risk. Thus the evolution of individual signatures in the advertisement calls (but not alarm calls) of the fathers.

Ten adult females were played advertisement and alarm calls from their genetic father and an unrelated male in this playback experiment. Nine of the females paid more attention to the advertisement calls of the unrelated male than to the father, but there was no difference in response to the alarm calls (with the females reacting to both callers). It seems that the advertisement calls of genetic relatives are similar, and this is how they are recognised as kin.

(Source: Gabriella Skollar)

Figure 1.3 - Grey mouse lemur.

1.2. MOTHERS

Among primates, there are different structures by which males gain access to females. One is hierarchy, where the dominant male has priority of access to fertile females. In this situation, competition between males produces the dominant individual, and the other males depart [4] or remain as submissives in the group.

An example of the latter is bonobos (Pan paniscus).

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[4] This is known as matrilocal or female philopatry (young males disperse and females remain).

High-ranking males sire more offspring (where this has been determined by DNA analysis) (eg: Gerloff et al 1999) [5]. But among bonobos, females also have rank. So high-rank mothers can help their lower rank sons to access mates through, for example, intervening in conflicts between males over females (eg: Surbeck et al 2011 [6]). The mothers benefit from such behaviour because any grandchild will carry 25% of their genes.

An alternative structure is egalitarian (ie: no rank) as in the northern muriqui monkey (Brachyteles hypoxanthus). Strier et al (2011) reported details of a long observed group in Minas Gerais, Brazil, whose biological relationships have been established through DNA in their faeces [7]. There is not aggression between males over females, and mothers do not directly intervene to help sons' access to females, but a pattern emerged that adult sons who remained physically closest to mothers were most reproductively successful [8]. It was not clear how the closeness to the mother aided reproductive success. Suggestions included time with mother helped the son to be more familiar with females, or to be aware when females are sexually receptive [9].

In egalitarian groups, brothers could work together to access females as any offspring of a brother (ie: niece/nephew) will carry 25% of shared genes.

1.3. APPENDIX 1A - SEXUAL CANNIBALISM AND AGGRESSIVE SPILLOVER HYPOTHESIS

One question often asked is why non-adaptive behaviours remain in populations despite their lack of benefit. One answer is that behavioural syndromes (or "personalities") may enhance individual fitness in one situation but not in another.

Rabanedo-Bueno et al (2014) used the example of sexual cannibalism [10]. This is where a female of the

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[5] The distribution of mating is skewed with dominant males accounting for the vast majority. Subordinates can challenge this situation by males (related or unrelated) forming alliances as the dominant male mate guards.

[6] Data from ongoing observations at Lui Kotala, Salonga National Park, Democratic Republic of Congo focusing on nine males. The presence of the mother clearly increased the mating success of low- and mid-ranking adult sons, but had no effect for high-ranking males. Surbeck et al (2011) pointed out that "females are able to engage in aggressive interactions with males without the high cost of injuries. One could also speculate that the presence of mothers reduces the probability of aggression by high-ranking males against their sons" (p595).

[7] Twenty-two infants were born between 2005 and 2007 to thirteen fathers during the study.

[8] The group is patrilocal or male philopatic (ie: young adult females disperse and males remain).

[9] Karen Strier (2012) quoted at http://www.scientificamerican.com/article.cfm?id=mom-is-my-wingman (last accessed 01/04/2015).

[10] This behaviour is present among some insects like the praying mantis, and some spiders and scorpions (Kralj-Fiser et al 2013).

species eats the male after copulation, and gains both sperm and food. But sexual cannibalism can occur before (or during) copulation, which is less beneficial. The latter behaviour could be a means of sexual selection (ie: eating only poor quality males before copulation) [11], or a product of the "aggressive spillover hypothesis" (ASH) (Arnqvist and Henriksson 1997), which sees some individuals as more aggressive than others [12].

Rabanedo-Bueno et al (2014) investigated these possibilities with ninety-nine male and eighty virgin female [13] Iberian Peninsula tarantulas (wolf spiders) (Lycosa hispanica) in southern Spain. Individual males were released into enclosures with females, and three possible outcomes were recorded - mating, cannibalism, or passive interaction (ie: male stands still when female present). The females were allowed to feed on beetles and woodlice (natural prey) as much as they wanted, and their weight gain was used as an indirect measure of the "personality trait" of voracity (or aggression).

Voracious females (ie: largest weight gain) were more likely to cannibalise males (ie: before mating) irrelevant of the male's size/quality [14], whereas less voracious females cannibalised poor quality males and mated with good quality ones. This supported the ASH. Voracity was beneficial in terms of weight gain, but detrimental in indiscriminate killing of suitors.

Among a funnel spider (Agelenopsis pennsylvania), about one-third of virgin females showed pre-copulatory cannibalism, but no female killed two successive males. In fact, these females had greater reproductive success than females that mated with the first male (Berning et al 2012). This suggested that pre-copulation cannibalism was related to mate choice rather than ASH (Kralj-Fiser et al 2013).

Kralj-Fiser et al (2013) were critical of the ASH - "we find it crucial to clarify the use of the terms sexual cannibalism (effect) and female aggressiveness or tendency to attack and devour males (cause). These terms should not be used interchangeably as sexual cannibalism

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[11] Also when males are abundant, females are hungrier (adaptive foraging hypothesis), or when females have already mated (Rabanedo-Bueno et al 2014). It could be due to failure to recognise a potential mate as well (Kralj-Fiser et al 2013).

[12] It is "a spillover of female aggressiveness from the juvenile foraging context, when aggressiveness is advantageous, to the adult mating context, when aggressiveness may be non-adaptive or maladaptive" (Kralj-Fiser et al 2013 p615). Thus, at the extreme, as seen in females of the fishing spider (Dolomedes fimbriatus), they risk remaining unmated (Kralj-Fiser et al 2013).

[13] Virgin females must weigh up the fact that they do not know how many males they will come (which encourages mating) against waiting for good quality males (which suggests eat poor quality ones) (Rogers 2014).

[14] The males were more likely to freeze in the presence of voracious females.

is a possible but not the sole consequence of female aggression. Indeed, there are several examples where females behave aggressively towards males, but if the male continues to court, copulation may still occur with or without a subsequent cannibalism event..." (p620). Female aggressive behaviour could be a way to test the persistence of males (and indirectly their quality).

For voracity (or aggression) to be seen as a "personality trait", Kralj-Fiser et al (2013) wanted to see certain things including individual differences in the behaviour within a population, repeatability of the behaviour by an individual, and control of other variables (eg: level of hunger of females) in experiments.

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2. TYPES OF PARENTAL CARE

2.1. VARIATIONS IN BEHAVIOUR

"Parental care, by definition, is any parental behaviour that increases offspring survivorship" (Bickford 2004 p402) [15]. Parental care varies depending whether the animal lay eggs (oviparity) or the embryo develops in the female (ovoviviparity) (Eisenberg 1981).

In the case of eggs, it includes protection from predators or pathogens [16], placing eggs in sheltered spot (concealed or disguised), on or near food, and/or guarding, maintenance of egg temperature, hydration (on land) or aeration (under water), and jostling (moving eggs around) (Bickford 2004) [17] [18]. Providing food for newly hatched/born animals can continue for a long period. In longer-lived animals (where generations overlap), parental care is beyond where offspring can obtain own food - eg: vervet monkey mothers protect adolescent and adult offspring from competition with older and dominant animals (Clutton-Brock and Godfrey 1991).

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[15] O'Connor and Shine (2003) defined it as "any behaviour by an individual that appears likely to increase the fitness of its own offspring" (p1361), while Royle et al (2012) referred to "any parental trait that enhances the fitness of a parents' offspring, and that is likely to have originated and/or to be currently maintained for this function".

[16] For example, egg guarding by frogs includes blocking access to eggs (eg: inflating body), attacking predators, and killing and eating them (Bickford 2004).

[17] Crump (1996) distinguished six types of parental care in frogs - egg attendance, egg transport, tadpole attendance, tadpole transport, tadpole feeding, and internal gestation.

[18] Female scorpions (Euscorpius flavicaudis) carry young on back from birth for seven days (Goodenough et al 1993).

Putting the different aspects of parental care together, the following categories can be distinguished (Clutton-Brock 1991):

a) Establish and maintain nests, burrows or territories [19].
b) Provide gamete only (ie: sperm or egg).
c) Care for fertilised eggs until hatch.
d) Care of offspring without provisioning (eg: guarding).
e) Care of offspring with provisioning.
f) Care after nutritional independence.

The need for some form of parental care depends on variables like the ability of the embryo to survive unattended or laid eggs to be undamaged, and how much care enhances survival. There are also costs for the carer (table 2.1) [20] including a trade-off between current and future reproduction [21] - eg: defending the young from predators increases the risk of death [22], or staying with the young reduces the opportunity to forage for the carer (ie: less opportunities for future reproduction) [23] [24] [25]. Parental care will evolve, then, if the benefits of care that increases offspring survival is greater than the cost to the parent(s) [26].

- A cost of parental care can be seen in predators deliberately choosing pregnant or egg-carrying females as prey. In these situations the female is often conspicuous and has reduced mobility.

- Li and Jackson (2003) showed the preference for egg-carrying females in interactions between two species of spiders - white-moustached portia spider (Portia labiata) (predator) and pale spitting spider (Scytodes pallida Doleschall) (prey). The latter female carries her fertilised eggs around until hatched. The predators were offered motionless lures of a dead egg-carrying or

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[19] But is this parental effort or mating effort (Barnard 2004)?

[20] For example, incubating eggs involves a heat loss to the parent. It was estimated that heat transfer to the eggs is the equivalent to 10-30% of parent's basal metabolic rate in some birds (Clutton-Brock and Godfrey 1991).

[21] "Contemporary reproductive value" (current brood) versus "residual reproductive value" (future offspring) (Trivers 1972). The differential allocation hypothesis is also relevant (appendix 2A).

[22] There are times when an animal is particularly vulnerable to predation, and these include when searching for, attracting/signalling, and courting a mate, actively competing with rivals, mating, and caring for young (Li and Jackson 2003). Parental presence when guarding may actually attract predators towards the young.

[23] For example, larger eggs laid leads to less laid, while increased laying rate produces smaller eggs in experiments with domestic chickens (Clutton-Brock and Godfrey 1991).

[24] This type of trade-off is important in life-history theory (eg: Gadgil and Bossert 1970).

[25] One cost of parental care is the vulnerability to grief if offspring dies (appendix 2B).

[26] It is often assumed that because the initial investment of the female is greater (ie: eggs), then maternal care is more likely. But this is not the case automatically because providing care is more investment and cost for the female (Alcock 2005).

eggless prey when placed at the bottom of a Y-shaped apparatus. The predators chose significantly more egg-carrying lures than eggless ones (58% of choices were egg-carrying vs 22% eggless vs 20% neither) [27]. The choice was not based just on conspicuousness of the egg-carrying as the experimenters varied aspects of the body sizes. Thus, they said, "we confirmed that, by sight alone and independent of movement-related cues, Portia labiata can discriminate between egg-carrying and eggless scytodids" (p134).

- In a survival test, equal numbers of egg-carrying and eggless white-moustached portia spiders were left in a large tank for twenty-four hours with the predator. The two groups of females were matched for body length. Significantly more eggless females survived (almost all vs 80% egg-carrying).

- The egg-carrying mothers do gain a benefit despite the increased cost in that eggs left unattended in webs are less likely to survive than when carried around (Li and Jackson 2003).

Table 2.1 - Example of cost of parental care.

Wojczulanis-Jakubas et al (2013) asked the key question: "When exposed to stressors, such as inclement weather, food deprivation or predation risk, breeding adults face a dilemma: should they continue caring for their offspring or should they abandon it, thereby securing their own survival?" (p448) [28]. If the current offspring is high value, then the parent(s) will take the cost to themselves. This is known as the "brood value hypothesis" (Wojczulanis-Jakubas et al 2013). The current offspring may be valuable because of the parent's age (ie: no future breeding opportunities) or because of environmental constraints (eg: problems finding future mate), for example.

Tallamy and Brown (1999) suggested that the evolution of care requires large benefits over no care and moderate costs, or moderate benefits with only low costs.

The latter is seen in the Hibiscus Harlequin Bug (Tectocoris diophthalmus) (figure 2.1), where females stay with clutches of eggs until hatching (about

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[27] Based on data in Li and Jackson (2003) table 2 p133.

[28] Lukas (2013) observed: "Pick up any current textbook on behavioural ecology, and you will find that the word 'family' is invariably followed by the word 'conflict''. Conflicts between family members arise because selection favours individuals aiming to maximize reproductive fitness, and these aims frequently collide because selection pressures differ even among related individuals. Offspring can improve their reproductive fitness by obtaining the maximal amount of investment from both of their parents. However, parents frequently provide less than the maximum because any increased investment into current offspring impacts their ability to produce additional offspring in the future. Caring for offspring in all its forms is energetically expensive and may impair a parent’s ability to have additional offspring in a variety of ways". For example, male European starlings (Sturnus vulgaris) who spend less time incubating eggs have a better chance of mating with a second female. While female golden egg bugs (Phyllomorpha laciniata) who lay their eggs on a male rather than on a plant give that offspring a better chance of survival, but such males have a greater risk of predation from birds (Lukas 2013).

seventeen days) and for a few days after. Giffney and Kemp (2014) studied guarded and unguarded clutches near the northern beaches of Sydney, Australia. In a laboratory environment (ie: no predators), there was no difference between the two groups (around 80% success). But in the wild, hatching success (defined as number of live nymphs that hatched divided by total number of eggs laid per clutch) was significantly less for unguarded clutches (about a quarter). Egg guarding stopped predators from eating the eggs, but not parasitoid wasps from laying their eggs inside the bugs' eggs. The mothers continued to feed during guarding, so "maternal egg guarding appears to function as a relatively low cost-low benefit strategy that increases hatching success by protecting against predation - but not parasitism" (Giffney and Kemp 2014 p607).

(Source: samfrasersmith)

Figure 2.1 - Adult female harlequin bug.

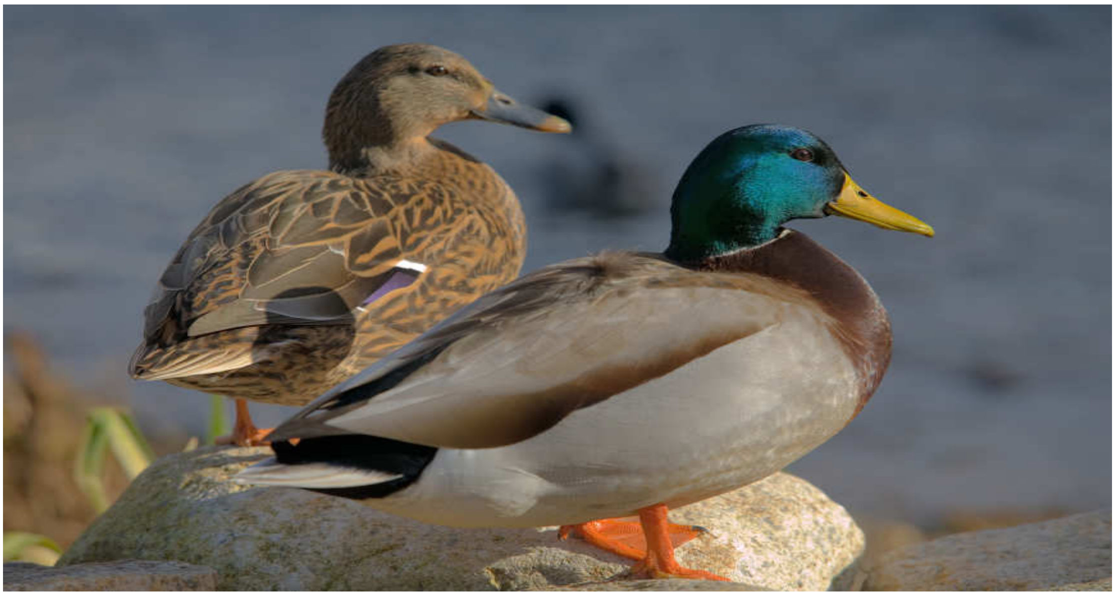
Wilson (1975) proposed four "prime movers" that influence whether parental care is provided or not:

i) Stable or well-structured environment.
ii) Unusually physically harsh environment.
iii) Specialised food resources - scarce or rare.
iv) Level of predation.

When parental care is provided, there is the question of how long should it continue. The cost-benefit trade-off of when to leave the offspring depends on weather conditions/food availability, offspring age, and the young's ability to survive on their own (Boos et al 2010). For example, female mallard ducks (Anas platyrhynchos) pay less attention to the brood as they age, and care ends at six weeks post-hatching, when the ducklings are almost the same size as the mother (though flightless) (Boos et al 2007).

The health of the mother is also important. Those in poor body condition are more likely to desert the brood in order to enhance their own survival (the "salvage strategy" hypothesis). Larger, more valuable broods are less likely to be deserted before "maturity" (brood size hypothesis) (Boos et al 2010).

In an experimental study, Boos et al (2010) found that broods of mallard ducks (figure 2.2) prematurely deserted by the mother (who is the sole carer) (ie: between 2-6 weeks post-hatching) (n = 35) had a 23% lower survival probability than matched broods not deserted (n = 36). Radio-tagged ducks in the Nord region of France were studied.



(Source: Diliff)

Figure 2.2 - A pair of mallard ducks.

Huang and Pike (2013) studied long-tailed skinks (Eutropis longicaudata) in south-east Asia. Most populations do not show parental care, but in one population, on Orchid Island, Taiwan, the mother guards the eggs during incubation. Data were collected on this latter population and compared to two non-care populations on other islands in Taiwan.

Huang and Pike (2013) assessed the factors involved in the evolution parental care with their data.

i) Harsh and unpredictable environments - Scarce food at the time of hatching should encourage parental care because the benefit of leaving the eggs is low. "However, if food resources are abundant at the time of nesting, an alternative hypothesis is that parents would not necessarily trade-off egg guarding with food searching. This would lessen the time spent away from the nest and provide the female with more energy with which to protect the nest. Parental care might strongly benefit egg survivorship in these instances" (Huang and Pike 2013). Huang and Pike's (2013) data supported the latter.

ii) "Risky" life history - "Short-lived species often have lower reproductive outputs than long-lived species, and thus could be more likely to pursue 'risky' reproductive strategies than long-lived ones. Parental care is a 'risky' behaviour because it can render the parents vulnerable to predators" (Huang and Pike 2013). Not supported by data.

iii) Exposed or hidden nest sites - It is predicted that well-hidden nests are less risky for the parents and so parental care will evolve. "Although long-tailed skinks bury their eggs beneath rocks in natural habitats, the eggs of females nesting inside the retaining wall [29] remain exposed during incubation. Females nesting in populations expressing or not expressing maternal care both nest in these retaining walls, suggesting that egg exposure in and of itself does not always lead to maternal care" (Huang and Pike 2013).

iv) Suitability of habitat for protecting eggs - Parental care will evolve where the eggs are laid in the animal's usual territory, and this familiarity should give protect from predators. Not supported by Huang and Pike's (2013) data as the nesting site was different to usual living area.

v) Ability of parents to defend nest - Parental care should evolve in species able to defend their eggs/young.

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[29] Eggs on Orchid Island were laid in nest within drainage holes running through a concrete retaining wall along a mountain road.

Long-tailed skinks on Orchid Island have relatively large body size and can defend against egg-eating snakes.

vi) Low reproductive frequency - A species that produce few offspring per breeding season are more likely to care for them (ie: more invested in each offspring). "The costs for long-tailed skinks to guard their eggs are minimal, and similar for females with both large and small clutches. Some long-tailed skinks reproduce twice within a single breeding season, and guard both clutches, which does not support this prediction" (Huang and Pike 2013).

vii) Brief incubation periods - Where incubation periods are short in length, parental care is more likely to evolve as less risk for carer. There was some evidence that the skinks on Orchid Island had quicker incubation than elsewhere. "However, the incubation period may not be a major factor in the evolution of maternal care in this species because females in populations with and without maternal care nest in two habitat types: some females bury eggs beneath the soil (where they are not visible to predators) and some females lay eggs inside of a retaining wall (where they are visible to predators. Furthermore, the duration of maternal care does not always last the entire incubation period, but can vary due to the frequency of attempted egg predation by snakes. Hence, this prediction may be overly simplistic" (Huang and Pike 2013).

viii) Increased egg hatching ratio - Parental care will evolve with higher egg hatching ratios (ie: more of laid eggs hatch). Skinks with maternal care had a higher egg hatching ratio.

Huang and Pike (2013) concluded "that the evolution of maternal care in long-tailed skinks is related to at least five different factors: the energetic investment in a clutch, the delay of future fecundity, the risk of predation to the parent, the ability to defend the eggs from predation, and the increase in hatching success provided by maternal care".

The direct benefits of parental care to offspring can be studied by adult-removal experiments. This is the removal of the carer to see how many offspring survive compared to when the carer is present. For example, Bickford (2004) removed adults (usually males) from one or two pairs of clutches of eggs of two species of frog in Papua New Guinea. The eggs of a terrestrial frog (Hylophorbus rufescans) experienced 100% mortality (compared to 22% when parent present) as did those of a tree frog (Oreophryne sp. "A" [30]) (which has no mortality with parental care) [31].

2.2. CHANGING AND MULTIPLE CARE

More than one pattern of parental care can be seen within a single population of a species during a single breeding season - eg: of 140 clutches of penduline tits (Remiz pendulinus) observed by Persson and Ohrstrom (1989), 48% female only care, 18% male only, and 34% none.

The type of care can vary because of time-dependent care decisions (changes in environmental conditions during breeding season), "quality" (ie: what is good quality in a species may include behaviour related to parental care or not, but, in the former case, quality can only be assessed after mating), or choice of nest site (eg: making poor choice with too many predators in the vicinity might make desertion a good strategy) (Webb et al 1999) [32].

The type of parental care can change during the period of offspring care. For example, the Arctic seabird, the little auk (Alle alle) (figure 2.3) changes from biparental to male-only care. Both parents incubate a single egg on the nest for the four weeks after laying, and then protect and feed the newly-hatched chick up to a few days before fledging. The female leaves, and the male continues to feed the chick until it leaves the nest colony (and possibly for a few weeks after at sea) (Wojczulanis-Jakubas et al 2013).

One explanation for this behaviour is that the male is more able to aid the first flight to sea, particularly as it is slightly larger than the female, it is able to protect against predators (eg: gulls).

It was proposed that males are, thus, less risk-

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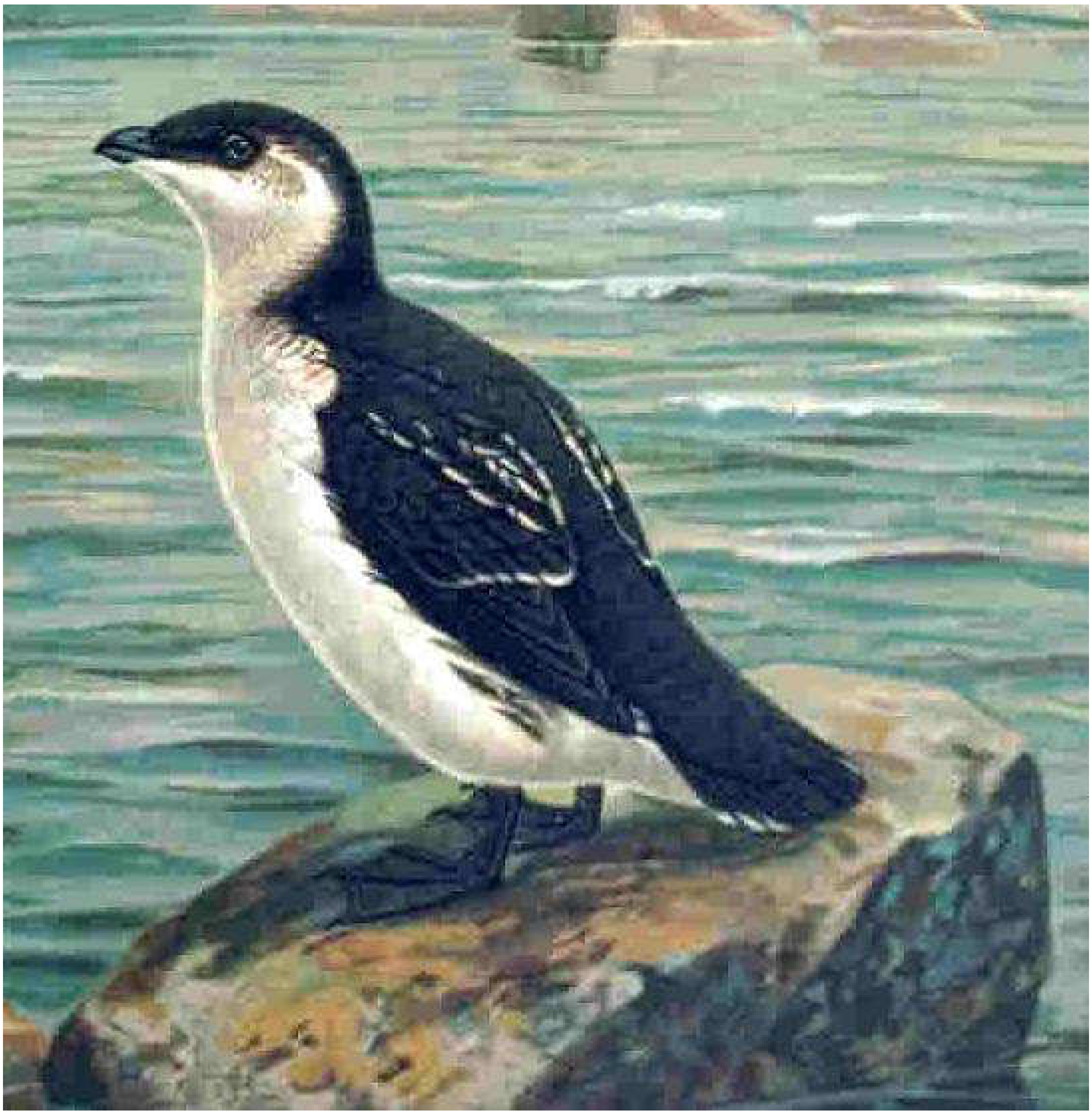
[30] Undescribed species at time of study (Bickman 2004).

[31] Parental care is provided by individual species in seventeen of 27 frog families, but this is less than 10% of all frog species (Bickman 2004).

[32] Webb et al (1999) also described this case: "Two birds are taking turns to incubate their clutch: one sits on the eggs while the other forages for food. While the male is out foraging, he uses the opportunity of repeated interactions with other females to assess the availability and qualities of potential new mates. How long he spends away from the nest and the proportion of time he spends foraging will depend on the overall availability of food, how successful he has been in previous foraging bouts and the rate at which he encounters females. The female has to decide how long she will continue to incubate in the absence of the male. If he delays his return too long, then the female may decide that he has deserted. If the female cannot successfully rear a brood on her own then she will desert (whether the male has, in fact, deserted or is just trying to rebuild his energy reserves during a particularly unsuccessful foraging bout). The length of time that a female may tolerate a male’s absence could depend on her own energy reserves (which determine how long she can risk going without feeding) and on her assessment of the general foraging conditions (which determines the likelihood that the male has actually deserted). This example shows how complex parental care decisions may be in reality..." (p989).

averse than females (ie: more willing to participate in the risky behaviour of predator protection), but Wojczulanis-Jakubas et al (2013) found no support for this in a novel object experiment. A bright piece of plastic was placed close to the nest to see whether the bird returning from foraging would be too scared to feed the chick. There was no sex difference in fear response to the novel object, which suggests that males are not less risk-averse.



(Source: Naumann "Natural History of Birds in Central Europe, 3rd ed" (1905); in public domain)

Figure 2.3 - Drawing of little auk.

The type of parental care also changes with evolution as can be seen if both types of care exists within a family of animal. For example, Gittelman (1981) identified 21 cases of switches in fish during evolution.

For example, eleven genora/families had changed either from male only care to no parental care or vice versa, but none had changed from both parents to none (or the other way), or from male only to female only (or vice versa) (Slater 1999).

2.3. TYPES OF PARENTAL CARE

Goodenough et al (2001) summarised the three theoretical models for the evolution of type of parental care.

1. Certainty of paternity hypothesis - greater certainty means greater likelihood of male care (as in external fertilisation).

2. Gamete order hypothesis - the sex that releases the last gamete will provide parental care. With internal fertilisation, this is female (ie: sperm goes to egg), while it is male with external fertilisation (ie: eggs left and sperm added).

3. Association hypothesis - the sex who is nearest to offspring at birth/hatching will provide care - ie: female with internal fertilisation and male with external fertilisation.

Table 2.2 summarises the different types of parental care and when they might evolve.

	Female cares	Female does not care
Male cares	Biparental - offspring survival must exceed uniparental care	Male uniparental - offspring survival greater than no care, and no alternative reproduction opportunities for male
Male does not care	Female uniparental - greater offspring survival than no care	No care - greater survival of offspring than care or cost of care too high

Table 2.2 - Different types of parental care and when expected.

2.3.1. No Parental Care

a. No contact with offspring - possible with external fertilisation as in fish like common cod (Gadus) which eject sperm and eggs into open water.

b. Permanent and immediate brood desertion - offspring left immediately at birth or when egg laid.

c. Permanent brood desertion after basic behaviour - eg: mother moves eggs to sheltered spot before leave.

Variation

i. Temporary brood desertion/absentee mothering.

For example, a hider strategy and absentee mothering, where the young are left by the mother hidden and she returns occasionally for nursing or in response to distress calls (eg: white-tailed deer; Odocoileus virginianus). European rabbit mothers (Oryctolagus cuniculus), who leave their young in a burrow and only return for a three-minute nursing once a day, take this type of care to the extreme (Rodel et al 2013).

The young are safe unless their hiding place is found, and the mother can spend the time foraging. With European rabbits there is a risk of infanticide as other females seek to use the burrow to give birth and raise their young, while many smaller predators are unable to access the burrow. To combat the risk of discovery, the young need to have a long-range alarm call to summon the mother, which Rodel et al (2013) showed in their playback experiments.

In a specially built enclosure at the University of Bayreuth in Germany, sixteen artificial warrens were created. Ten-second recordings of pup distress calls were played to mothers individually when they were ten metres away from their burrow. Response behaviour by the mother was scored as raising head while feeding (vigilance behaviour) or returning to explore burrow. A tone was used the control sound. It was a repeated measures study, and the control sound was always played first (with a thirty-minute gap before the call). Mothers were tested once a year.

After playback of the distress calls, 70% of mothers showed vigilance behaviour compared to 25% to the control sound (p<0.001) [33], while 60% returned to the burrow (vs 9% for the control sound) (p<0.001). The time after birth did not influence the results (3-6 days vs 12-16 days post-partum).

To sum up: "Female rabbits with dependent offspring responded strongly to the playback of pup distress calls by returning to their breeding burrow and extensively monitoring the entrance and surrounding area. This behaviour occurred in a high proportion of mothers during the early as well as during the later post-partum

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[33] Using the statistical test chi square (X^2) (appendix 2C).

period" (Rodel et al 2013 p1029).

ii. Give birth to adult offspring - eg: aphids give birth to clones of mother at start of season, and these daughters have female offspring in womb at their birth [34].

iii. Matriphagy - hatched offspring cannibalise mother (who chooses not to escape) - eg: Black lace-weaver spider (Amaurobius ferox).

Advantages	Disadvantages
* Parents more opportunities for future reproduction, and no loss of resources on current batch/offspring. * No risks in defending against predators. * No energy use on feeding.	* Best when many offspring (fecundity), and so low survival rate not important. * Offspring must be born/hatch well developed and able to fend for themselves. Also low risk of predation (eg: toad tadpoles taste nasty). * Risk of inbreeding if parents remain in geographical proximity.

Table 2.3 - Advantages and disadvantages of no parental care.

Examples:

- Mammal - Probably unlikely as mammals born relatively helpless and need feeding.
- Bird - Megapode mothers (eg: Australian brushturkey; Alectura lathami) bury eggs before leaving, and geothermal heat incubates them.
- Insect - More common as young born relatively mature.
- Fish - Many because of external fertilisation.
- Other - Female leatherback sea turtles come ashore to lay eggs in then sand and then leave after covering them.

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[34] "Attenborough's Natural Curiosities: Virgin Births" (2014) UKTV.

2. One Parent Alone (uniparental) [35].

a. Mother

Cockburn (2006) defined female-only care in birds as when "males usually do not feed at any nest but are occasionally observed to deliver a small amount of food late in the period of parental care when no other mating opportunities are available" (p1376).

Post-birth maternal care varies greatly, even between close species. For example, of nearly 8000 species of scarab dung beetle which use dung in which to lay eggs, less than 1% provide maternal care (Tallamy and Brown 1999).

b. Father

More common among fish species that provide parental care, and many insects.

For example, female sticklebacks are drawn to egg-guarding males (Alcock 2005).

While male frogs that guard clutches of eggs until they hatch, allow females to mate again. Thus, protecting against the risk of extinction (Platt 2014).

Male fish lose less than females from providing parental care. For example, stickleback males can care for ten clutches of eggs to hatching over two weeks whereas females can produce a maximum of seven clutches in the same period (even without providing care) (Clutton-Brock and Parker 1992).

While female caring mouth-brooding cichlid, St Peter's fish (Serotherodon galilaeus) are slower to produce a new clutch of eggs to mature than female non-parents (24 vs 13 days) (Balshine-Earn 1995). Either sex can mouth-brood in this species.

Variation

i. Care in part - For example, female scarlet crabs on Christmas Island wait with fertilised eggs for two weeks and then release them into the sea to fend for themselves. It is estimated that a female can produce about one million eggs over ten years (Attenborough 1992).

Female Ammophilia (caterpillar-hunting) wasps shock

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[35] For example, among Membracinae (treehoppers), Lin et al (2004) calculated that maternal care evolved three different times, but never paternal care, suggesting that maternal care evolves more readily.

the burrow with immobilised caterpillars (food) and then seal in young before leaving (Attenborough 1992).

ii. Definition problems - eg: polygynous birds where the male feeds the young of the first female but not those of his other females (Cockburn 2006). Is this uniparental (mother) or biparental?

iii. Caring for offspring selectively - eg: preference for firstborn.

Advantages	Disadvantages
* Caring parent increases chance of offspring survival and subsequent mating. * Less individuals in each brood if greater chance of survival. * Deserting parent can find other matings.	* Caring parent has less opportunities for future matings. * Risk in protecting offspring. * Deserting has no knowledge of how many offspring survive.

Table 2.4 - Advantages and disadvantages of uniparental care.

Examples:

- Mammal - Female uniparenting common, but paternal uniparenting unlikely because young require milk.
- Bird - Painted snipes (Rostratulidae) male care. Hummingbirds (Trochildae) and manakins (Pipridae) (female-only) (Cockburn 2006). Male American jacana (Jacana spinosa) builds nest and cares for offspring (Jenni and Betts 1978).
- Insect - Male Giant water bugs (Lethocerinae) brood eggs laid on vegetation (Smith 1997) [36].
- Fish - Most often male egg guarding, but maternal egg guarding in blennies as all eggs laid in single clutch in short breeding season. Where males externally fertilise several females, and there is the risk of egg cannibalism or female competition also leads to female uniparental care (Clutton-Brock and Godfrey 1991).

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[36] But a reluctant father as the female puts sticky eggs on the male's back before leaving (Attenborough 1992).

- Other - Floating rocket frog (Silverstoneia flotatos): mother transfers eggs to male before leaving (Lukas 2013).

2.3.3. Both Parents Together (biparental)

Evolved because more offspring survive than with uniparental care, and/or a deserter unlikely to find another mate.

Commonly among birds - Cockburn (2006) estimated that 80% of bird species have biparental care (8% female-only; 9% co-operative care; remainder are no care, male-only, or brood parasites).

Owens (2002) proposed the low-density hypothesis, where male care is provided if the geographical density of individuals is low and there is little opportunity to find an alternative mate if they desert brood.

Where there are two parents involved in caring, this "creates the potential for conflict between the parents because it is advantageous to minimise one's own investment while capitalising on the benefits that arise from the investment of the partner" (Bulla et al 2014 p152). This conflict can be resolved by each parent providing a fixed amount of care (eg: each parent incubates eggs for half the time), or a "behavioural negotiation" between the parents (Bulla et al 2014).

Bulla et al (2014) continuously video monitored monogamous pairs of semi-palmated sandpipers (Calidris pusilla) in high-Arctic Alaska for six weeks to see how the parents divided the 21-day incubation period (ie: sitting on the eggs in the nest). The observation period was divided into five-second segments for fifty-one nests (total = over 8.9 million segments).

The average female bout of incubation was 11.5 hours compared to 10.7 hours for the male. Though the females spent longer on the nest, they were "compensated" by foraging more often during the warmer part of the day. The timing of the shifts also varied over the incubation period (eg: evening-night to night-morning) in most pairs.

However, the variety of behaviour between the pairs suggested that "behavioural negotiation" was taking place in some way. For example, among some pairs, one bird always did the "night shift" and the other bird the "day shift". Among other pairs, the length of incubation bouts changed, and this "allowed both parents to experience similar incubation/off-nest conditions but during different days within the incubation period" (Bulla et al 2014 pp160-161).

But if both parents try to exploit the another (ie: leave the heavier workload to the other parent), the offspring will suffer. The above cases are evidence of the evolution of "negotiation rules" that "work", but sexual conflict is still in many cases.

Iserbyt et al (2015) investigated this in experiments with Fife Fancy canaries (Serinus canaria) (figure 2.4) kept at the University of Antwerp, Belgium. Half the nests were allocated to female uniparental care and half to biparental care for fourteen days after hatching. The chicks from uniparental nests were significantly heavier at the end of this period, and this was because feeding effort was much lower per parent in biparental nests. Begging for food by the chicks was significantly more in biparental nests. Feeding was biased towards already heavier chicks here.

(Source: Haplochromis)

Figure 2.4 - Fife Fancy canary.

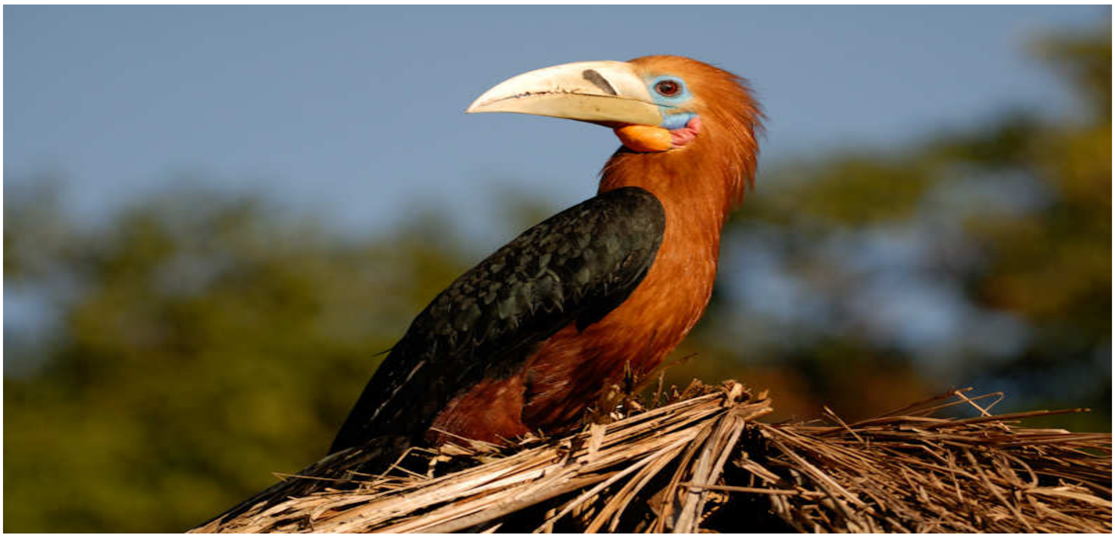
On two days the biparental nests were split between the parents who were placed in adjacent cages (visible partner condition) or in separate rooms (invisible partner condition). In the latter case the male parent provided more food than the female parent. The researchers interpreted this behaviour as due to the asymmetry in information about the brood between the parents. Females spend more time near the nest traditionally and have a better picture of the brood's health. It was noted that "well-informed females do not work harder but keep private information and exploit their partner when they are out of sight. Why females do not exploit their mate permanently is likely to depend on the balance between mate exploitation and the female's urge to respond to increased offspring begging behaviour" (Iserbyt et al 2015 p56).

Iserbyt et al (2015) felt that their results showed "the existence of a costly sexual conflict over parental care". When controlling for equal potential workload, the mothers in the uniparental nests provided twice as much food per offspring than each parent in the biparental nests. The researchers stated: "Specifically, we indicate that uniparental females may opt to invest more in the quality of the current brood when they rely only on themselves at the onset of the breeding period. This increased current investment is expected to lower the female's general condition and may therefore be at the expense of future reproductive investment and lifetime fitness... Such trade-offs remain speculative and require further attention, but they may well hamper the evolution of uniparental care" (Iserbyt et al 2015 p56).

Variation

i. "Quasi-biparental care" - one partner deserts before care complete.

ii. Female cares for offspring and male feeds them - eg: the female rufous-necked hornbill (Aceros nipalensis) (figure 2.5) imprisons herself in a tree cavity with eggs and then hatched offspring while male brings food (Poonswad 2002).



(Source: User: Kalyanvarma)

Figure 2.5 - Immature male rufous-necked hornbill.

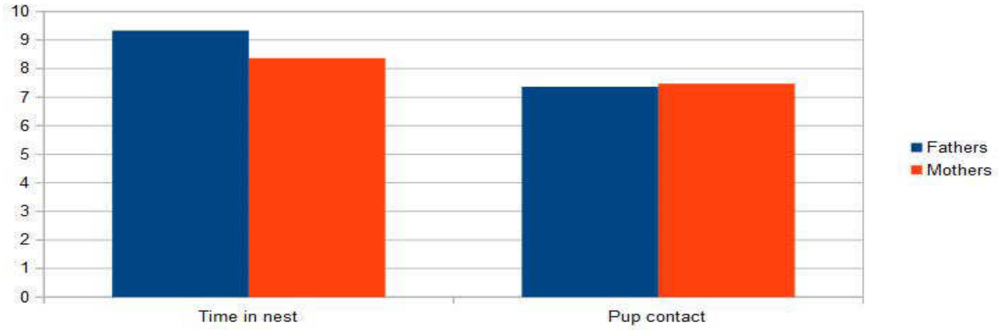
iii. Nuclear family but no care [37] - Indirect parental care can be seen in female lizards that protect a territory and the offspring that happen to live within it are protected from infanticide. Describing their work with black rock skinks (Egernia saxatilis), O'Connor and Shine (2004) noted that "parents did not behave differently when their offspring was present (even when it was being attacked); their sole 'parental' behaviour was tolerance of the juvenile's presence" (p1366).

Advantages	Disadvantages
* Less work per parent and more provisioning. * Certain behaviours possible - eg: guarding and feeding. * Little opportunity for other matings if desert.	* Whether on parent doing more than the other. * Uncertainty of paternity (ie: males caring for offspring that not their own). * Costs incurred caring for current offspring.

Table 2.5 - Advantages and disadvantages of biparental care.

Examples:

- Mammal - California mouse (Peromyscus californicus) - Gubernick and Alberts (1987) were the first to detail the biparental care from thirty-one days of observations of six pairs and their young in the laboratory. Males and females performed all parental activities and to the same extent (except lactation). There were slight variations in the licking of the pups (figure 2.6).



(Data from Gubernick and Alberts 1987 table 1 p175)

Figure 2.6 - Amount of behaviours by mothers and fathers (in hours and minutes) on Day 5.

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[37] Black rock skinks live in "nuclear families" (O'Connor and Shine 2003).

- Bird - Many examples (up to 90% of bird species; Wesolowski 1994), particularly where mother stays at nest and father collects food [38].

- Insect - Not common, but more likely in terrestrial arthropods (eg: beetles) (Zeh and Smith 1985) [39] - eg: Korean wood-feeding cockroach (Cryptocercus kyebangensis) (Park and Choe 2003).

- Fish - Striped goby cichlid (Eretmodus cyanostictus). This is monogamous mouthbrooding cichlid in which the female (1st 8-12 days) and male (10-16 days) brood the clutch.

Gruter and Taborsky (2004) set up an experiment to compare pair brooding with female-only. The offspring in the latter condition were smaller and less developed at release from mouthbrooding. Lone females prolonged their incubation period, but did not entirely cover the period when the males would usually be involved. The lone females' weight dropped by 15% during incubation (ie: not eating at this time) compared to 7% with a partner.

The researchers observed that all the females waited about twenty days from the end of her incubation period until the next spawning. In evolutionary terms, the male improves his offspring's survival by brooding rather than not while waiting for the next spawning. Thus, a possible explanation for the evolution of biparental care in this species. But a male could look for other females during the waiting time instead. This is risky if there is a male-bias sex ratio (ie: more males than females) (Gruter and Taborsky 2004).

- Other - Unheard of in reptiles (Wesolowski 1994).

2.3.4. Both Parents and Helper(s)

Distinction between "obligate co-operative breeding" where the young cannot be reared by unassisted parents, and "facultative co-operative breeding" where assisted occurs sometimes (Ligon and Burt 2004).

"Helpers" may be a consequence of non-dispersal of adolescents and non-breeding adults, so do they really

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[38] But "divorce" among socially monogamous birds is quite common (appendix 2D).

[39] Common characteristics of insects with biparental care include females usually stay in nest and nest has limited access that can be defended by male. Thus biparental care may have evolved for males as an extension of mate guarding (Suzuki 2013). Also, for example, nest cleaning by the male bark beetle does not increase offspring survival, but it enhances certainty of paternity (Lissemore 1997).

help? Emlen (1991) proposed three ways to answer this question.

i) Helpers increase breeding couples' reproductive success.

- Simple correlations between number of helpers and number of offspring surviving to reproduce are positive - eg: silver-backed jackal (Canis mesomelas); red-cockaded woodpecker (Picoides borealis). But controlling for variables (eg: age of breeders) reduces the effect.

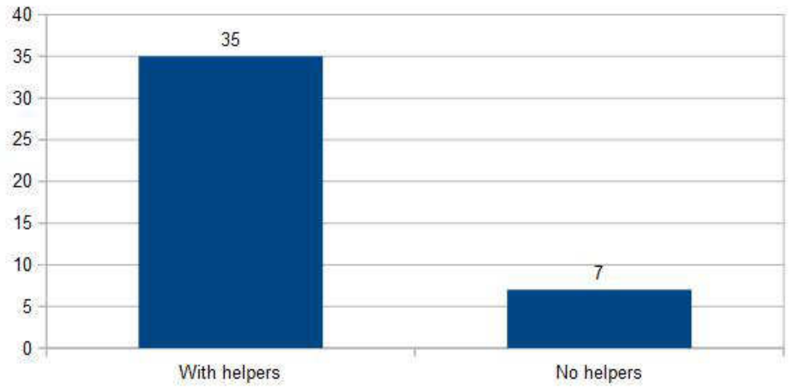
- Removal of helper experiments show differing results - breeding success declines without them (eg: grey-crowned babblers; Pomatostomus temporalis) vs does not decline (eg: moorhens; Gallinula chloropus)

ii) Helpers actually reduce "workload" of breeding couple.

iii) Helpers improve survival of breeding couple to reproduce in future.

a. Kin

Birds - Florida scrub jay (Aphelocoma coerulescens) raise young with breeding pair and help from full or half siblings. Mumme (1992) found that five times more offspring survived to sixty days after hatching in nests with helpers compared to no helpers (experimentally removed by researcher) (figure 2.7).



(Data from Ridley 1995 table 10.2 p242)

Figure 2.7 - Percentage survival of offspring in nests with or without helpers.

Birds with delayed dispersal and breeding may remain with parents when mature, but they are not all helpers (eg: Australian magpie, red kite) (Ekman 2006).

b. Non-kin

"Additional attendants" - eg: Non-breeders or failed breeders among Adelie penguins huddle, shelter, and defend young generally, or when white tern (Gygis alba) parents are absent, other adults and juveniles may preen and brood chicks (Cockburn 2006).

Variation

i. Father and male helpers - eg: white-throated brown hornbill (Ptilolaemus tickeli) (Poonswad 2002).

Advantages	Disadvantages
* Less work for parents. * Kin helpers gain as they share genes with offspring. * Non-kin helpers gain opportunity to learn about parenting.	* Non-kin helpers may be restricted from breeding themselves. * Non-kin helpers share no genes with offspring. * Helpers can be burden as extra mouths to feed.

Table 2.6 - Advantages and disadvantages of helpers.

Examples:

- Mammal - Geoffroy's tamarin (Saguinus geoffroyi) (Cooke et al 2008).

- Bird - fairy-wren (Malurus cyaneus); mousebirds (Coliidae) (Cockburn 2006).

Shane (2010) reported seeing an adult Pine Siskin (Carduelis pinus) feeding two begging fledgling House Finch (Carpodacus mexicanus) in his garden in Kansas, USA. Skutch (1961) would describe such Pine Siskin as "breeding unilateral interspecific helpers", while Brown (1987) referred to "interspecific alloparenting by mistake".

2.3.5. Communal (alloparental care)

There are four types of communal care (Gittelman 1985):

i) Nuclear family with reproductive pair and offspring from previous seasons - eg: beaver.

ii) Matriarchy with reproductive female only - eg: little brown bat.

iii) Harem - eg: Northern elephant seal.

iv) Multi-male/multi-female group containing both related and unrelated individuals - eg: lions.

a. Kin

This can be quite similar to parents with a helper, except that both biological parents may be involved in care.

Wheaton et al (2013) reported the first case of alloparental care by a captive Key Largo woodrat (Neotoma floridana smalli) at Disney's Animal Kingdom, Florida, USA. A juvenile/sub-adult female was seen to assist her mother with birth and care of a new litter. The animals were continuously video-recorded, and the researchers were able to score the maternal behaviour (eg: grooming pups) for the first thirty days. Using instantaneous-scan focal sampling, the juvenile female's behaviour was categorised every two minutes (as maternal or non-maternal).

The mother benefited by being able to leave the nest (which was twice as much as a mother without assistance). The presence of the helper may stop the pups from calling out when the mother absent (which could attract predators), and from leaving the nest too early. The helper gained parental experience.

b. Non-kin

eg: ostrich and joint nesting.

Female mammals provide nutrients to their offspring via milk (lactation). This is costly for the mother (in terms of energy required, survival, and future reproductive success). So, why do lactating females sometimes feed non-genetic young ("alien offspring") (known as allosuckling or allonursing) [40]. "Even if milk production does not entail any fitness penalty, nursing activities directed towards unrelated offspring would also be selected against to prevent unrelated individuals

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[40] Fostering has been reported in over one hundred mammal and bird species (Schneff 2004).

from spreading more gene copies in a limited population" (Roulin 2002 p201).

Allonursing has been observed in 68 species of mammals, particularly among those who share roosts (eg: bats), those who reproduce communally (eg: lions), or give birth in confined spaces (eg: seals) (Roulin 2002).

Roulin (2002) reviewed five hypotheses proposed to explain allonursing:

1. Misdirected parental care hypothesis - Alien offspring are fed by mistake [41] (ie: mother does not notice) or by "theft" (ie: allosucklers steal milk) [42]. For example, among certain close-living seals (eg: northern elephant seal; Mirounga angustirostris), alien offspring push off pup who is drinking milk and take over, and sometimes the mother does not notice (Reiter et al 1978). However, among these same seals, females will kidnap pups to adopt (Roulin 2002).

2. Reciprocity hypothesis - Two communal living females share the feeding/care. But how does each female know that the other is doing their fair share? A "cheater" female (feeds offspring less) will get greater benefits.

3. Kin selection hypothesis - Mothers nurse alien offspring who are genetically related - eg: mice (Mus domesticus) have higher reproductive success in nests with two sisters than two unrelated females (Konig 1994). Also related non-reproductive females benefit if they feed the young (ie: shared genes with nieces and nephews, for example).

But they are examples of allonursing of non-genetic relatives (eg: grey seals) (Roulin 2002).

4. Milk evacuation hypothesis - Allosucklers receive surplus milk that the mother's offspring did not consume. The mother gains by evacuating the surplus milk - eg: among northern elephant seals, fat reserves (used to make milk) make the animal buoyant and less able to dive for food (Roulin 2002).

5. Parenting hypothesis - Inexperienced females allonurse to practice or improve their maternal skills. Thus it should be young or inexperienced females who do

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[41] It is a "reproductive error" (Schneff 2004).

[42] Lewis (2004) distinguished milk "theft" from communal nursing.

it. But "in studies in which the age of allonursers was known, young females did not nurse alien offspring more frequently than old ones" (Roulin 2002 p205).

Roulin (2002) felt that evidence from wild populations of different species supported the misdirected parental care, kin selection, and milk evacuation hypotheses only (table 2.7).

Hypothesis	Species
Misdirected parental care	Support - 3 species (eg: Asian water buffalo; Bubalus bubaris)
Reciprocity	Not supported - 3 species (eg: lion)
Kin selection	Supported - 4 (eg: lion; Panthera leo) Not supported - 4 species (eg: Asian water buffalo)
Milk evacuation	Supported - 1 species (evening bat; Nycticeius humeralis)
Parenting	No evidence either way

(Based on Roulin 2002 table 1 p205)

Table 2.7 - Studied mammal species and hypotheses for allonursing.

Variation

i. Part-time communal care: A female eider duck sits on her eggs (and gets hungry). When young mobile, they are put in "creche" with other young and non-breeding birds. The mother goes away to feed, but returns to do "nursery duties" (Attenborough 1992).

Advantages	Disadvantages
* Less work for parent(s). * Allows parent(s) to go away for while to feed (or mate again). * Improved survival of own offspring in group (eg: thermoregulation, dilution effect).	* Effort to care for non-kin (eg: lactation costly to mother). * Some individuals may not do their share of communal care ("freeriders"). * Less resources available for own offspring (eg: milk).

Table 2.8 - Advantages and disadvantages of alloparental care/communal care.

Examples:

- Mammal - Packer et al (1992) analysed ninety-two questionnaires from biologists working with mammalian species, who were asked about the proportion of time that young nursed from lactating female other than own mother.

About one hundred species - more likely in captive animals [43], those with larger litter sizes (eg: pigs, rodents), and in single offspring species (monotocous [44]) who lost offspring.

- Insect - Common among social insects who very closely genetically related.

- Other - Taita African caecilian (Boulengerula taitanus) (Kupfer et al 2008) (figure 2.8).

(Source: Milvus)

Figure 2.8 - African caecilian.

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[43] "This supports the contention of several authors that non-offspring nursing often appears to be an artefact of disturbance, crowding or captivity.. It also suggests that non-offspring nursing is more common in conditions where females have access to unlimited food" (Packer et al 1992 p267).

[44] Polytocous = more than one offspring born at same time.

2.3.6. Brood Parasitism/Egg Dumping

Social or brood parasitism (or egg dumping) is where the host raises the offspring of the parasite instead of or as well as their own. Lyon and Eadie (2008) noted: "Parental care is costly... It comes as little surprise, then, that various forms of reproductive parasitism have evolved that enable individuals to gain the many benefits of parental care while avoiding the substantial costs and constraints" (p344).

a. Own species (Conspecifics brood parasitism; CBP)

Over 200 species of birds (eg: grebes, swallows) (Lyon and Eadie 2008).

CBP harder to spot and study than IBP (eg: different shaped or sized eggs to host) (Lyon and Eadie 2008).

Lyon and Eadie (2008) outlined four types of theories for CBP in birds:

i) Best-of-a-bad-job - Poor environmental conditions limit breeding options, so IBP better than no offspring in that breeding season.

ii) Nest loss - Similar to above.

iii) Lifelong specialist parasites - Females that on use IBP.

iv) Fecundity enhancement - Bypass the constraints of parental care on clutch and brood size (eg: more clutches in breeding season with IBP).

Sorenson (1991) distinguished four strategies for birds - non-breeding, all by IBP (non-nesting IBP), all own nest, and combination of IBP and own nest (nesting IBP) (table 2.9). The first two strategies are low reproductive investment, and are more likely when there is low success in nesting or high cost of reproduction. Different environmental conditions will influence which strategy used.

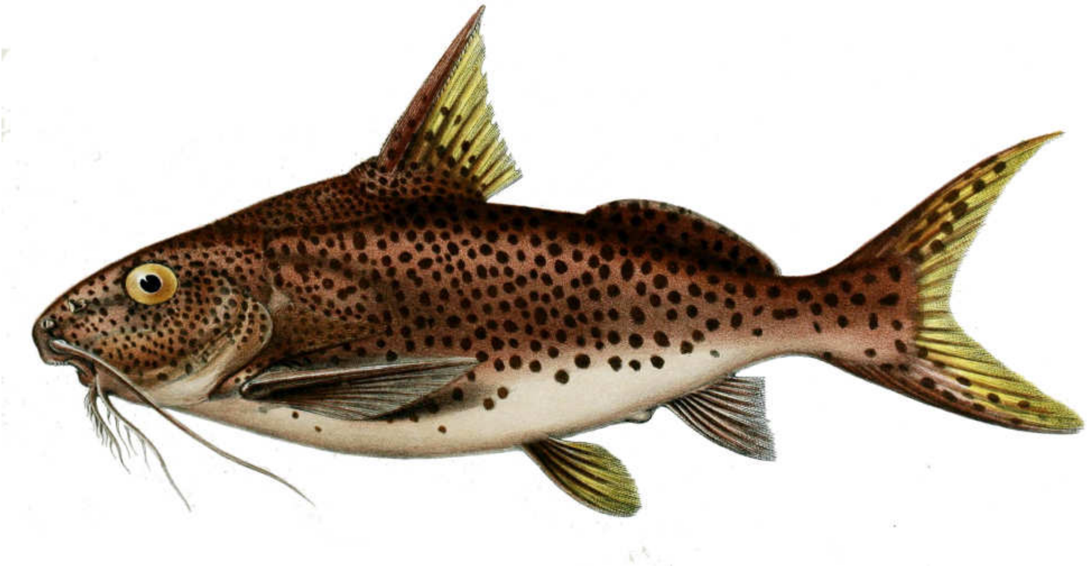
b. Another species (Interspecific brood parasitism; IBP)

Cuckoo catfish (Synodontis multipunctatus) (figure 2.9) leave their eggs near mouth-brooding cichlid eggs. The cuckoo catfish adults attack the female cichlid, and she picks up as many eggs as possible into her mouth including cuckoo catfish ones (which are brooding by the cichlid) (Cook et al 2008).

NON-NESTING	NESTING
• Avoid cost of nesting/parental care (increased current fecundity). • Females unable to acquire nest (increase own survival). • Females in poor condition (increase own survival). • Better offspring survival in another nest.	• Nest loss (increased current fecundity). • Bypass constraints on number of offspring (increased current fecundity). • Reduce parental care needed by placing some eggs in another nest (increase own survival).

(Based on Lyon and Eadie 2008 table 1 p348)

Table 2.9 - Nesting and non-nesting IBP in birds.



(Source: Green (1898) Transactions of the Zoological Society of London, volume 15; in public domain)

Figure 2.9 - Drawing of cuckoo catfish.

Advantages	Disadvantages
* No cost of parenting. * Suitable for females without territory where egg dumping is better than no egg survival. * More eggs together reduces predation risk for each egg.	* Mother has no control over offspring's survival. * No guarantee of survival. * Risk from host's offspring.

Table 2.10 - Advantages and disadvantages of brood parasitism.

Examples:

- Bird - 57 species of brood-parasitic cuckoo have been distinguished, of which twelve are found in Australia, fifteen in Africa, and about 26 in Asia (Heberstein et al 2014). About 100 species of birds that use obligate IBP (ie: never have nest of their own) (Lyon and Eadie 2008).

2.3.7. Other

a. Adoption of non-kin

Atkinson et al (1996) reported the case of an adult female polar bear in Canada, who had lost cubs, adopting three other apparently non-kin cubs. Non-kin adoption is seen to have costs to the carer while only benefits to the adoptees. The benefit to the carer could be in gaining experience of raising young.

Atkinson et al (1996) noted: "...as polar bears do not typically raise their offspring under social conditions, selective pressure for a well-developed mechanism of mother-offspring recognition may be relatively weak... Consequently, the potential for misidentification and adoption of non-kin may be significant at times when the offspring of a number of females are in close proximity" (p95).

Males who care for non-kin could be advertising to females that they will be good future fathers. For example, in the fish, redlip blenny (Ophioblennius atlanticus atlanticus), males caring for eggs (not necessarily their own) attracts females to add their eggs to the nest. Santos (1995) removed twenty lone male carers from their nests, and other (non-kin) males adopted the fry because twelve of sixteen nests taken over received additional eggs from females.

b. Babysnatching

Variation - Cross-fostering experiment (appendix 2E).

2.4. APPENDIX 2A - DIFFERENTIAL ALLOCATION HYPOTHESIS

The differential allocation hypothesis (DAH) proposes that individuals vary their parental investment based on the current mate's quality [45]. For example, an

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[45] "This is based to the assumption that heritable quality ('good genes') will increase offspring value

individual will invest less in the current offspring (eg: providing less food) with a low-quality mate, and save their "resources" for future mating opportunities. On the other hand, more will be invested in the current offspring from a high-quality mate.

Most studies have looked at females varying their parental investment based on the male's attractiveness/quality (eg: Sheldon 2000). But males also vary their investment based on female attractiveness.

For example, Burley (1988) experimentally varied the attractiveness of female zebra finches (Tacniopygia guttata) by varying the appearance of black leg rings (female ornamentation). Males paired with more attractive females collected more food for their offspring than with less attractive females. Other studies have not fully supported the DAH for males (Mahr et al 2012).

Among blue tits (Cyanistes caeruleus) (figure 2.10), ultraviolet (UV)/blue crown coloration is a sign of quality [46]. Females adjust their egg quality, feeding effort, and nest defence of offspring based on the crown UV reflectance of the male partner (eg: Szigeti et al 2007).

Mahr et al (2012) found similar differences in investment by males paired with experimentally altered females. Birds captured near Vienna, Austria, were used in the experiment. Nineteen females were allocated to the UV-reduced group where the UV reflectance of the crown plumage was lowered by about one-tenth with a UV-blocking chemical. Eleven females were the control group with no alteration to UV reflectance. The parental investment of the male was measured by observation on day 13 after hatching. The number of feeding trips and the average prey size were recorded during one hour of observation. Nest defence behaviour was tested by introducing a rubber dummy snake predator close to the nest, and, for fifteen minutes, the number of attacks by the male was recorded.

Males paired with UV-reduced females performed significantly less feeding trips per nestling per hour than those with control females. There was no difference in the nest defence by males paired with either type of female.

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and eventually result in more grand offspring and, consequently, higher fitness. Consequently males should invest more in offspring provisioning when paired with ornamented females if male provide parental care and female quality strongly affects offspring survival" (Mahr et al 2012).

[46] High UV reflectance is a signal of nutritional status, and of time spent in plumage maintenance (eg: removal of dirt and parasites). "Individuals need to invest time in feather maintenance to keep their feathers in good condition. Plumage maintenance is a costly and time-consuming process, which forces individuals into a trade-off between plumage maintenance and time they need for other activities (eg: foraging). Hence, it could be that only individuals in good condition can afford these costs and therefore high UV reflectance" (Mahr et al 2012).

(Source: Gothika)

Figure 2.10 - Blue tit.

2.5. APPENDIX 2B - GRIEF

Video recordings of the reactions of chimpanzees to the death of an ageing female chimpanzees ("Pansy") at a safari park in Scotland in 2008 raised the question of grief among non-human animals (Anderson et al 2010). The chimpanzees showed behaviours including pre-death care (grooming and caressing in ten minutes preceding death, but no grooming after death), close inspection for signs of life at death (equivalent to testing for pulse or breath by humans), aggression towards the corpse (similar to attempted resuscitation by humans), and subsequent avoidance of the place where death occurred.

Other observers also report chimpanzees mothers continuing to groom their dead infants (Sample 2010).

Bottlenose dolphins (Tursiops truncatus) have been observed interacting with dead members of their pod [47], while elephants react in a certain way when they find elephant bones (Hooper 2011). Among primate observers in the wild, Jane Goodall, for example, described the decline and death from grief of a young male chimpanzee soon after the death of his mother (King 2013).

Hooper (2011) noted: "Interpreting animal behaviour after death of a companion is fraught with difficulty. Death is rarely observed in the wild, and it is easy to erroneously attribute human emotions to animals". But social animals appear to show particular behaviours when an animal dies, which could be "akin to mourning" (Hooper 2011).

A simple definition of grief requires a relationship between animals beyond survival-oriented behaviours, and that "when one animal dies, the survivor alters his or her normal behavioural routine - perhaps reducing the amount of time devoted to eating or sleeping, adopting a body posture or facial expression indicative of depression or agitation, or generally failing to thrive" (King 2013 p52).

2.6. APPENDIX 2C - CHI SQUARE

Chi square calculates whether the observed data were statistically significantly different to chance.

Table 2.11 uses data from Rodel et al (2013) and the response of rabbit mothers to an alarm call.

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[47] Joan Gonzalvo reported a bottleneck dolphin mother continuing to care for a dead newborn calf for two days off the Greek coast. King (2013) responded: "Was the dolphin mother truly grieving for her dead calf? A decade ago I would have said no. As a biological anthropologist who studies animal cognition and emotion, I would have recognised the poignancy of the mother's behaviour but resisted interpreting it as mourning... Now, though, ...I think Gonzalvo was correct in his judgment that the mother dolphin was mourning" (p52).

	Alarm call	Control sound	**Column Table**
Number of mothers showing vigilance behaviour	23 cell A	10 cell B	**33**
Number of mothers not	8 cell C	25 cell D	**33**
Row Total	**31**	**35**	**Grand Total** 66

Table 2.11 - Data matrix for chi square.

$X^2 = \sum$ (sum of) $(O - E)^2 \div E$

where:
O = observed data
E = expected data by chance; calculated as:
Row Total x Column Total ÷ Grand Total

Cell	O	E	O-E	$(O-E)^2$	$(O-E)^2 \div E$
A	23	15.5	7.5	56.25	3.6
B	10	17.5	-7.5	56.25	3.2
C	8	15.5	-7.5	56.25	3.6
D	25	17.5	7.5	56.25	3.2
X^2					**13.6**

Table 2.12 - Calculation of X^2.

To see if the calculated value of X^2 (13.6) is significant, it is necessary to compare the figure to the critical value. In a table of critical values, 10.83 is the figure for a two-tailed hypothesis at $p<0.001$ with df = 1. Df is the degrees of freedom, which is calculated as the number of columns of data minus 1 x number of rows of data minus 1 (ie: 2 -1 x 2 - 1 = 1). The calculated value should be equal to or greater than the critical value to be significant.

2.7. APPENDIX 2D - DIVORCE AND SOCIALLY MONOGAMOUS BIRDS

Mating systems can be classed as social or genetic. The social mating system is based on the observed "patterns of pairings between sexes, and their share in the care of offspring" (Culina et al 2014). For example, social monogamy (or biparental care), which is common among birds, is where a pair remain together for a breeding season (or more). The genetic mating system focuses on the genetic parents. So, one member of a socially monogamous pair could have extra-pair matings. It is estimated that 85% of bird species are socially monogamous, but of these, only about a quarter are genetically monogamous (Culina et al 2014).

Social monogamy can break down with the death of one partner (widowing), or "divorce", defined as "when re-mating with a new partner occurs for at least one member of a surviving pair" (Culina et al 2014). Divorce has been reported in over 90% of socially monogamous birds (Culina et al 2014). But is divorce beneficial to socially monogamous birds?

Culina et al (2014) sought to answer that question with data from eighty-one studies of wild populations of sixty-four socially monogamous birds. The measure of the benefit of the behaviour is breeding success, which can be assessed in different ways, including clutch size (ie: number of eggs laid) or fledging success (ie: eggs that hatch and offspring leave nest).

If divorce is an evolutionarily adaptive strategy individuals will have higher breeding success after divorce than before, and than faithful pairs. Divorce was found to be adaptive for individuals when triggered by low breeding success (ie: birds that later divorce had lower breeding success compared to faithful pairs), and when earlier in the breeding season (as measured by laying date). Females benefited more than males in terms of increasing breeding success subsequently.

In the season after divorce, divorced birds had lower breeding success than faithful pairs, but higher than the pre-divorce season. "This would mask an improvement in breeding success between the two seasons when only measuring breeding success after divorce... there might be costs of partner change (eg: one partner is inexperienced with the site, or the co-ordination between pair members is sub-optimal...) which obscure the signs of improvement if breeding success is measured and compared to faithful birds in the breeding season after divorce only" (Culina et al 2014).

Divorce can have disastrous consequences if there are no males or females available (Sarchet 2014).

2.8. APPENDIX 2E - CROSS-FOSTERING EXPERIMENT

The question of nature or nurture haunts the understanding of behaviour. In reality, it is difficult to distinguish the two elements of genes (nature) and environment (nurture) [48]. One method to do so is the cross-fostering experiment. This is where the young of one group or species are reared by another group or species that is different. Any behaviour that the adoptee shows particular to their group is seen as inherited, and any behaviour in common with adopted parents is learned (figure 2.11).

Figure 2.11 - The logic of the cross-fostering experiment.

In an example of cross-fostering, Slagsvold and Wiebe (2007) transferred the eggs of blue tits (Cyanistes caeruleus) to the nests of great tits (Parus major), and vice versa, in woodland near Oslo, Norway.

The researchers focused on feeding behaviour [49], which shows a difference between the two species. Blue tits feed on caterpillars high in trees, while great tits mainly on the ground. For example, if blue tits raised by great tits foraged high in trees, then the behaviour is innate. But if they forage on the ground, then the behaviour is learned.

The cross-fostered birds showed the behaviour of the foster species, but the effect was stronger for great tits [50]. Slagsvold and Wiebe (2007) concluded that "the foraging behaviour of the parents, and possibly other individuals perceived as conspecifics, seemed to be imprinted on the young ones, probably because juveniles

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[48] Though a behaviour is inherited, it could still be flexible (ie: modified by learning). It may be better to distinguish behaviours as inherited/fixed and inherited/flexible. Another variable is when the behaviour is fixed - before/at birth, or during a critical or sensitive period in early life. Furthermore, attempts to determine nature or nurture tend to ignore the pre-natal situation. Is what happens in the womb (or pre-hatching) nature or nurture? Researchers tend to ask how much of behaviour is down to nature or how much is down to nurture, rather than nature or nurture, if they ask anything now.

[49] A species will find a unique niche in the face of competition from other species, according to ecological theory (eg: feeding from a particular section of a tree, or feeding from the same source at different times).

[50] The birds were observed in early autumn as they became independent, and in spring before breeding started.

avoid costly trial-and-error learning by copying behaviour that has proven to be successful for their parents" (p21).

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