Parental Care and Investment

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Parental care is common throughout the animal kingdom and among caring species there is a bewildering variation in how parents care for offspring, as well as in the amount of resources parents invest in care. For instance, there is considerable variation in the relative parental investment by the sexes – in some species females invest more, in others males invest more, and in some investment is more or less equally shared. Different hypotheses have been proposed to explain patterns of parental investment between the sexes, as well as among species, and work is still ongoing to develop an overarching hypothesis that can explain the various patterns observed.

Definitions of Parental Care and Parental Investment

Possibly as a result of human infants’ utter dependence on parental care during its early infancy, we do not tend to view the investment of valuable resources by parents towards feeding or tending to their offspring as an evolutionary puzzle. However, the question of why parents invest resources, which could be used to better their own condition and probability of survival, on their offspring is far from trivial. Indeed, among animals there is a wide variation in the type of care and amount of resources that parents invest in the offspring. In many species, investment is limited in producing eggs or live offspring, which are then left to fend for themselves – for example, in the herring (Clupea harengus), whereas in other species both parents invest in substantial periods of parental care, sometimes even after nutritional independence, as in several bird species and some mammals including humans.

Parental care is defined as any form of parental behaviour that increases the fitness of the offspring. This definition of parental care includes preparation of nests and burrows, production of large, heavily yolked eggs (which are generally associated with increased hatchability and survival of the young), care of eggs or the young inside or outside the parent’s body, provisioning of young before and after birth and care of the offspring after nutritional independence. Two contrasting categories of care exist, though many forms may lie between the two extremes: depreciable care, such as provision of food, where the benefits of parental care decrease for individual offspring as the brood or litter size increases; nondepreciable care, such as parental vigilance to detect potential predators, where the offspring’s individual benefits do not decrease with increasing brood or litter size.

Parental investment, however, is defined as any expenditure by parents on an individual offspring that reduces their potential to invest in other present and future offspring. The definition of parental investment is a subject of discussion and problems often arise concerning what should and should not be included. Today, the term is generally used to refer to any action of parents that increases the fitness of their offspring at the cost of the parents’ future reproduction. This definition highlights the
conundrum presented by parental investment, as parents face a trade-off between investing resources in their own survival or future reproduction and investing these resources to increase their current offspring’s chances of surviving and reproducing. It is important to note that there is no necessary correlation between the size of parental investment in an offspring and its benefit for the young, the currency of interest is the cost to the parent in future reproduction.

Three Key Questions of Care: ‘To Care or Not Care?’, ‘Who Should Care?’ and ‘How Much?’

Research into parental care and investment can be summarized by three main questions.

Why do not all species care for their offspring?

Parental care requires resources from parents which then cannot be invested in their own growth, survival or future reproduction. Because resources and time are limited, parents face a trade-off regarding where their investment should be directed, whether towards their offspring or themselves. Thus, from an evolutionary point of view, parental care is expected to be favoured only when the benefits to parents, and not necessarily to the offspring, outweigh the costs. This is an important, albeit complex point because parental care will be favoured as long as it results in an increase in the parent’s fitness, which generally tends to coincide with the interests of the offspring, though not necessarily without conflict. However, for the parent if the costs of care exceed the benefits, that is, the cost to the parent’s future reproduction becomes higher than the benefits the parent may gain through the offspring’s increase in future reproduction as a result of the investment, the parent will curtail care, even if this is detrimental to the offspring. In several species, the offspring hatch or are born at an excessively early stage of development and unable to survive without parents providing food, shelter and protection from predators. This is the case, for example, in birds whose chicks hatch naked with eyes closed (altricial species) and in most mammals. In such species, the benefits of care clearly outweigh the costs as parents not providing any care will have no progeny. Parental care is also favoured when environmental conditions are harsh, when the risk of predation is high and when there is strong competition for resources. See also: Parent–Offspring and Sibling Conflict

Which parent should provide care – the male, the female or both?

Early hypotheses to explain sex differences in parental investment were developed in part focusing on the general mammalian tendency of higher investment by females. This high prevalence of care by females was suggested to be a result of the initial differential investment by the sexes in terms of gamete size and number (anisogamy). Since females invest more energy in the production of fewer, larger eggs than males do to produce many, smaller sperms, female care would be favoured. Hence, as the argument went, females would stand more to lose if they did not invest in the offspring as a result of their higher initial investment. Males would, thus, show greater readiness for reproduction than females, which was proposed to result from the fact that while a male mammal’s essential role in reproduction generally ends with copulation, for the female copulation may result in a potentially protracted period of parental investment. This argument was later generalized emphasizing the need to consider all the means by which each sex contributes towards increasing the fitness of the offspring, which was combined in the term ‘parental investment’ presented in the preceding sections of the article. The relative difference between the sexes in parental investment was proposed to explain the patterns of competition between members of one sex for access to members of the other sex, mating competition, and hence the intensity of sexual selection. This ‘parental investment hypothesis’ proposed that the sex investing less in the offspring would have to compete for the sex investing more. The ensuing intrasexual competition for access to mating partners would, in turn, select against parental care by the competing sex because any amount of time or energy devoted to caring for the offspring would tend to decrease an individual’s chances of mating with other partners. The end result is one sex which predominantly competes for matings but does not invest, or invests very little, in offspring-care and the other sex which is choosier regarding partners and invests more in the progeny (Table 1). Note that the parental investment hypothesis assumes that parental investment patterns determine the sexual selection patterns (Figure 1). However, this hypothesis was criticized, since there was no reason why a high initial investment would select for higher investment in the future. Furthermore, the parental investment hypothesis cannot explain why male-only care is the norm among majority of the caring fish species. See also: Sexual Selection

The aforementioned hypotheses have the underlying assumption that differences in gamete size and initial investment are sufficient to explain why one sex competes and the other cares. However, since every offspring has only a single mother and a single father, the total number of matings in which males and females engage cannot differ. Hence, anisogamy does not generate an inherent bias towards care by one sex if both sexes have equal prospects of reproduction, which is generally the case in populations with equal numbers of adult females and males. What counts is the proportion of sexually mature individuals of each sex which actually participate in breeding, because it is only these individuals that face the choice (from an evolutionary point of view) between caring and abandoning.
Table 1 Hypotheses proposed to explain differences between the sexes in relative parental investment

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Short description</th>
<th>Support and criticism</th>
</tr>
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<tbody>
<tr>
<td>Anisogamy</td>
<td>Differences between the sexes in gamete size lead to differences in relative parental investment</td>
<td>No reason why high levels of initial investment should favour higher investment later on</td>
</tr>
<tr>
<td>Parental investment hypothesis</td>
<td>Extends anisogamy explanation to include broader definition of parental investment. Relative differences in parental investment between the sexes determine sexual selection</td>
<td>Criticism above applies to this hypothesis also. Further, it cannot explain observed patterns where the sex caring for offspring also competes more intensely for mates</td>
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<tr>
<td>Internal versus external fertilization</td>
<td>Proposed initially to explain care patterns in fishes, proposes that internal fertilization will favour maternal care whereas external fertilization will favour paternal care</td>
<td>Data from fishes seem to support it, but it cannot explain variation in care patterns in birds, all of which present internal fertilization</td>
</tr>
<tr>
<td>Sexual selection</td>
<td>Proposes that relative differences between the sexes in the intensity of sexual selection will determine parental investment patterns</td>
<td>Has the important advantage of assuming no initial bias between the sexes in the amount of investment. Incorporates information on adult sex ratios and operational sex ratios. Supported by one empirical study so far</td>
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Figure 1 Alternative evolutionary paths from a state of biparental care and moderate sexual selection to a state of uniparental care (in this example, female only care) and intense sexual selection acting on the noncaring sex. The first evolutionary path ((a)–(c)) involves initially a transition in the type of care, from biparental to uniparental, followed by a transition in the intensity of sexual selection acting on the noncaring sex. This follows what would be predicted by the parental investment hypothesis. The second evolutionary path ((d)–(f)) conversely, predicts first a transition in the intensity of sexual selection acting on one sex, followed by a transition in the care-type. This follows what would be predicted by the sexual selection hypothesis.

their partner to search for more mating opportunities. Therefore, recent hypotheses take into account the number of sexually mature members of each sex that participate in mating, and the costs and benefits associated with care for both sexes, assuming no initial bias by one sex to invest more in care. According to these recent hypotheses, the ratio of fertilizable females to sexually active males (termed operational sex ratio) and sexual selection through
introsexual competition or mate choice, result in differences between the sexes in the probability of encountering other partners and in the amount of investment each sex will be favoured to provide (Figure 1). For example, if some males are better competitors and are thus able to out-compete other males, or are more attractive to females, they could gain higher fitness by investing less in parental care if this allows them to obtain more matings. Note that the same scenario may apply to females and that in some species, like the broad-nosed pipefish (Syngnathus typhle) and jacana (Jacana jacana), females compete over males and males provide the care. Furthermore, in species where the females mate with many males, uncertainty of paternity favours less care from males, since the risk of caring for someone else’s offspring greatly increase the potential cost of caring. Under this ‘sexual selection hypothesis’ of relative parental investment, biparental care can also be explained, since under an equal adult sex ratio, with a low intensity of sexual selection acting on both sexes, increasing investment in care by both sexes would be favoured because of the low probability of encountering other mates (Table 1). On a more general note, biparental care is generally common in species where the offspring are highly altricial and require substantial amounts of post-hatching care to survive (like in many bird species).

How much care should be invested?

Regardless of which parent invests in care, there is a fine line between the benefits gained from parental care and the costs associated with the investment, thus parents are expected to optimize their investments to obtain maximal returns. Life-history traits will have an important influence on the amount of care parents will be selected to invest. This is of particular interest in relation to the trade-off between current and future reproduction. The relationship between parental care investment and life-histories can be shown by an empirical example. North American passerine species generally have higher adult mortality and lay larger clutches than closely related South American species, which have longer lives and lay smaller clutches. An elegant experiment compared the reaction of parents from five pairs of closely related species when a brood or an adult predator dummy was placed near their nest. In both cases, parents reduced nest visits to minimize the risk to their offspring or themselves. However, North and South American species differed. In the North American species, the decrease in nest visits was sharper when a nest predator was presented whereas in the South American species, the decrease was sharper when a predator targeting adults was presented. Hence, the results suggest that, as would be predicted by life-history theory, the North American birds do more to reduce risk to their offspring (placing higher value on current reproduction) whereas the South American species do more to promote their own survival (placing higher value on future reproduction).

Among species, females also face the conundrum of how to allocate their investment: that is whether to invest in a large number of small eggs (or offspring in live-bearing species) or invest in few large eggs (or offspring), sometimes referred to as the quantity versus quality trade-off. Species generally either lay large clutches of small eggs or small clutches of large eggs, although again there is variation among even relatively closely related species. Among the cardinalfishes (family Apogonidae) some species, like the Banggai cardinalfish (Pterapogon kauderni) lay a small clutch of only 50 large eggs (c. 3 mm) whereas the similarly sized pyjama cardinalfish (Sphaeramia nematoptera) lays a clutch of thousands of much smaller eggs. Moreover, body size may affect such a trade-off. In Galliform birds (wildfowl), females from larger species lay heavier but not more eggs than females from smaller sized species. In African cichlid fish, females from larger species lay much larger clutches of slightly larger eggs than females from smaller sized species. Hence, being large or small can affect how successful a certain strategy is in terms of the egg size – clutch size trade-off. Larger eggs or larger clutches also tend to be associated with more care, possibly as a result of higher requirement for their survival or because of the higher value of a larger clutch or a clutch of larger offspring.

Finally, the benefits of parental care to parent generally decrease as the amount of care invested increases. As the period of care progresses, selection will favour a decrease in care because this would reduce the costs to the parent’s future reproduction. Such a reduction in care is favoured because as the offspring develop and grow, their dependence on the parent(s) for survival and future reproductive success decreases, and hence, the benefit for parents of investing in future care also decreases. For very young offspring, a little amount of food can have a large impact on their survival, for the nearly independent young that same amount of food may have only little impact. However, things are rarely simple, and as the interests of parents and offspring do not always coincide, this can lead to conflict. Because parents are investing in their progeny, which in sexually reproducing species is related to the parent by on average 0.5 (i.e. a sexually reproducing parent shares on average 50% of their genes with their biological offspring) the benefit to parents of any investment in their offspring is devalued by a factor of 0.5. In other words, the gain in fitness to the offspring resulting from parental investment must be devalued by a factor of 0.5 because the offspring only carries, on average, half of the genes of the parent. The offspring receiving investment, however, is related to itself by 1.0. Thus, all other things being equal any investment by the parent is worth more to an offspring than to the parent. This may lead to conflict between parents and offspring in the optimal amount of investment in care (termed parent–offspring conflict). Conflict may also arise between parents regarding how much each should invest in the offspring. From an egoistic point of view, it is more advantageous for one parent to have its partner invest more in their offspring, since then it has to provide a smaller share of the total care; however, if both parents reduce care the offspring may suffer which would be detrimental to both. See also:
Parental Investment Patterns across Species

Among invertebrates, such as the terrestrial arthropods, care of eggs or offspring is rare and few orders actually present care of eggs or young. In the early vertebrates, for instance, the chondrichtyans (sharks and rays), parental care after the eggs or the young are detached from the parent’s body is absent. Conversely, approximately 21% of the 422 families of bony fish (Teleostei) show some type of care of eggs, including development of eggs or offspring inside the female’s body (ovoviviparity and viviparity), whereas fewer than 6% also show guarding of newly hatched young. Among amphibians, some sort of parental care (including ovoviviparity and viviparity) occurs in approximately 71% of the amphibian families, and 66% of them present care of the eggs or offspring by one of the parents. In reptiles, 56% of all families present some sort of care of eggs (including viviparity) whereas egg guarding by females occurs in approximately 3% of egg-laying snakes and 1% of egg-laying lizards. Parental care of eggs occurs in all bird species, although in some brood parasites (e.g., cuckoos) females have other species brood their eggs and feed their young, whereas the birds of a single family (the megapodes, Megapodiidae) do not incubate eggs themselves, but rather build mounds or bury them and the chicks hatch at an advanced stage of development and generally independent. Finally, all mammals provide care for offspring.

Among species with parental care, there is much variation in which sex is the primary care giver. In mammals, the overwhelming majority of species present female-only care, with fewer than 5% presenting biparental care. In birds, biparental care is much more common, with about 90% of the species presenting care by both parents even though females generally invest more into care than males. In fishes variation is much higher, with the majority of caring species (61%) presenting paternal care, 39% of the species presenting maternal care and roughly 20% species presenting biparental care (note that the species with biparental care are also represented in the species with maternal and paternal care). In fishes, sex differences in relative investment in care have been proposed to be influenced by whether fertilization is internal (which is associated with female-only care) or external (more generally associated with male-only care). Moreover, male territoriality, common in fish, has been proposed to favour the evolution of male care since it offers a transition into also defending eggs within the territory. Among amphibians parental care of eggs or young is commonest among terrestrial breeders in the humid tropics, and egg guarding, often by the male, is the most common form of care. The caecilian Boulengerula taitanus (a legless amphibian) presents a stunning example of parental care, where females develop a modified outer skin to provide a rich supply of nutrients for developing offspring to feed on. In reptiles, some lizard species care for eggs and pythons incubate the eggs for some time. Only crocodiles and their relatives care for both eggs and hatchlings.

Avoiding Misdirected Investments

Because of the elevated costs associated with parental care, selection has in some cases favoured the evolution of adaptations to avoid misdirected investments. Very good examples of such adaptations can be found in some colonial species (that is species which form large aggregations, termed colonies, to reproduce) most likely since they face a higher risk of the parents accidentally caring for someone else’s offspring. For example, to avoid misdirected investment, several species have developed complex offspring recognition mechanisms. The Mexican free-tailed bat (Tadarida brasiliensis) forms the largest mammalian colonies in the world and thus, the risk of mistaken identity of the offspring is very high. In this species, females use vocal and olfactory signals to locate their offspring when returning to the colony to feed them. Comparisons between colonial nesting swallows and solitary nesting ones showed that chicks from the colonial species produced more structured, distinctive calls, probably facilitating recognition by parents. Also, colonial cliff swallows are much better at discriminating their own young from conspecific young than solitary nesting barn swallows are.

Caring for Unrelated Young

In some species such as ducks, geese and swans, adults sometimes do provide parental care to unrelated young. Such cases range from creching behaviour, where chicks from several broods group together and are cared for by one or a group of parents (not necessarily the parents of any of the chicks) to true adoptions, which involve successful breeding pairs adopting one or more offspring into their brood, for which they assume all aspects of parental care while remaining a family unit. In several species, adoptions have also been documented involving same-sex parents, which successfully cared for the adopted offspring to independence. And in some cases, same-sex mates were even observed repeating adoptions during several reproductive seasons. Investment in unrelated young is a puzzling behaviour because selection would be expected to act against individual expenditure of resources in an individual with whom no genes are shared. Several hypotheses have been proposed to explain such behaviours. First, in the case of waterfowl, since chicks are precocial (i.e. hatch at an advanced stage of development, with feathers and able to feed themselves) the only parental care required involves keeping warm during nights or inclement weather and protection from predators. Hence, adoption of unrelated young may involve minor costs to parents and include some advantages for example by increasing brood size the risk of
predation to individual chicks is reduced through a dilution effect, because the number of potential victims increases. It is also possible that adoption is simply maladaptive behaviour resulting from a simple rule of thumb on which adults are acting. For example, if a young chick follows you, take care of it. Such simple rules of thumb might be sufficient to favour adaptive parental care in species where brood switching by young chicks or other types of parental care parasitism is rare. This is so because the alternative of developing mechanisms of parent–offspring recognition may involve steep costs, which might not be offset by avoiding the rare adoption or parasitism event.

In several species parents do not care for their young alone but receive assistance from helpers, which may or may not be related to the parents. Helpers may assist parents in defending the territory, protecting and feeding young. In these cooperative breeders, helpers are sometimes young from previous reproductive events, which remain within the parent’s territory and assist with care of siblings. Several explanations for cooperative breeding have been proposed. First, if helpers are related to the offspring, for example if they are full siblings, then they could gain through indirect fitness since full siblings share on average half of their genes. Second, if breeding territories are scarce, helpers could remain in the territory of a breeding pair, exchanging help for the right to remain within the territory while waiting to inherit that same territory. Finally, helpers, whether related or not, could also gain by gaining necessary experience in parental care. See also: Fitness; The Evolution and Ecology of Cooperative Breeding in Vertebrates

**Having Others Care for One’s Young**

Because parental care is costly, selection would favour individuals who are able to reduce the costs of care without incurring a reduction in their reproductive success. An excellent example of such cost-cutting behaviour is brood parasitism, where adult females lay their eggs in the nests of other females and have them feed and tend to their chicks. Brood parasitism occurs both within species (intraspecific parasitism) where the ‘parasitic’ female is from the same species as the host, and between species (interspecific parasitism) where the ‘parasitic’ female is from a different species as the host. The best known example of interspecific brood parasitism is the cuckoo family of birds, where 53 of the 136 species of cuckoos are specialist brood parasites, meaning that they always have other parents care for their young. Cuckoos have developed complex behaviours to maximize their chance of success, including egg mimicry, where the eggs have evolved to appear very similar to those of their host, and call mimicry, as in the Horsfield’s bronze-cuckoo (Chrysococcyx basalis), whose chicks can imitate the begging calls of host nestlings. Brood parasitism generally imposes elevated costs on the hosts since in some species, the cuckoo chick expels all host eggs from the nest, ending up alone and receiving all parental care. In other species, the early hatching cuckoo outgrows its host nestmates, which often starve. The obvious question is since hosts face such steep costs from parasitism – why not reject the parasite’s eggs or abandon a clutch that has been parasitized? This is an ongoing field of research and different explanations have been proposed. Host species may simply be unable to expel the parasites’ egg or there may be high costs associated with brood abandonment, an obvious one being the probability of committing a mistake and expelling one’s own egg or abandoning a brood which had not been parasitized.

**Care and Cognition**

Care of one’s own offspring can possibly also result in elevated cognitive demands on caring adults, as shown by two studies comparing various species of canids and African cichlid fishes. Both studies analysed the factors associated with differences in the relative brain size (brain size after correcting for differences in body size) of species. The studies compared species where females provided most or all of the parental care with species where care was shared by both parents. Interestingly, both studies found that females had larger relative brain size in female-care species than in biparental care species, which suggests that uniparental care may indeed have selected for increased cognitive ability in females.

**Within-species Variation**

Even within species not all the offspring are equal! Parents sometimes bias investment and care to offspring based on signals from their mate or from the offspring. For example, female mallards (Anas platyrhynchos) lay larger eggs, which have higher hatching probability and contain more nutrients, when they are paired with more attractive mates. And in the Banggai cardinalfish (Pterapogon kauderni), males brood the eggs in their mouths, and females lay larger eggs when paired with larger, higher quality fathers. Blue-footed boobies (Sula nebouxii) are marine birds, which typically lay 1–3 eggs and provide a prolonged period of biparental care. Both sexes choose their mate based in part on the colour of the potential mate’s feet, which may vary between a yellow-green and a dark blue-violet colour. Feet coloration has been shown to be associated with adult condition: dark blue feet signals bad condition whereas yellow-green signals good condition. Both sexes would be favoured to choose a mate in good condition because such a mate is more likely to invest more in care of the offspring than a mate in bad condition (the later would tend to value more its own survival as these are long-lived species). Experimental evidence shows that female blue-footed boobies adjust investment in their eggs based on the colour of the feet of their partner, decreasing the size of their eggs when the colour of the male’s feet is experimentally altered to signal bad condition (i.e. the feet are painted dark blue).
Adjustment in parental investment also takes place at the parental care stage as shown by zebra finch (Taeniopygia guttata) females which invest more into the care of offspring fathered by attractive males. Alternatively, it has been suggested that when unable to reproduce with a preferred partner, because of social or ecological factors, individuals may compensate for likely offspring viability deficits by investing more in that particular reproductive event.

Parents may also bias food delivery to specific offspring within a brood or litter based on signals provided by the progeny themselves, such as the vigorousness of their begging calls and the colour of the skin inside the beak (their gape coloration). Much study has been invested into determining to what extent begging and gape coloration are effectively honest signals of nestling condition. Honesty of a signal is essential if it is to be used by the receiver as a reliable indicator, in the case of begging or gape coloration reliable indicators of nestling condition. Because resources are limited, and energy must be invested to collect food for offspring, parents might bias food allocation towards healthier or stronger nestlings, which will make better use of extra food than a sickly sibling. If begging or gape coloration indeed signals condition parents should preferentially feed chicks with more conspicuous displays. Studies having tested whether parents distribute food among nestlings based on the intensity of their begging calls generally find this to be the case. With regards to gape coloration some studies have indeed found that chicks with more colourful gapes are fed more, and that gape coloration is partly dependent on nestling condition. However, there is also evidence suggesting that gape coloration might simply serve as a visual signal to parents for the location of their nestlings’ beak. See also: Parent–Offspring and Sibling Conflict; Signalling and Reception

Who should provide the care?

Regarding the questions of who should provide the care and to what extent, as mentioned earlier, theoretical and empirical studies have recently revisited the hypotheses proposed to explain which sex invests in parental care. The prevailing explanation based on anisogamy has been questioned and a recent empirical study with African cichlid fish lends support to the ‘sexual selection’ hypothesis for parental investment, as it showed that the type of parental care (in the species studied, only female or biparental care are present) is dependent on the intensity of competition between males for access to the females (see Figure 1). One of the underlying assumptions of the anisogamy-based hypothesis for parental investment is that any investment in searching or competing for mates is traded off against parental care. However, as mentioned above, in many fish species males compete for mates even though they are responsible for parental care. In some species, the amount and quality of care that males provide to the eggs or the offspring is a key trait used by females to assess the quality of these males. More work is needed to determine to what extent a trade-off does exist between investments in attracting or competing for mates and parental investment, especially since some behaviours influence both simultaneously. For example the quality of a territory defended by a male could influence both his success in attracting females, as well as offspring survival and future fitness. In several insects, males provide nuptial gifts to females, which are used to assess male quality as well as investing the resources into egg production. Hence, both territorial defence and nuptial gifts can be viewed as parental investments by the males and may at the same time be under sexual selection. To explain parental behaviour in both sexes, hypotheses are now being developed which assume no pre-existing bias by any sex towards higher parental investment, since for every offspring that has a single father and a single mother, there is no inherent bias towards care by one sex if both sexes have equal future prospects of reproduction. The many levels of variation in parental care among animals suggest that a multilevel approach, combining within-species behavioural studies, among-species comparative analyses and a genetic and genomic approach, is the best way towards determining the ultimate causes of the extreme variations that exist in care patterns among contemporary animals. Moreover, a largely missing part of the puzzle is the understanding of the genetic mechanisms of the displayed variations in parental care behaviours. Given the recent developments in the field of genetics and genomics, this approach may provide a novel tool in investigations of parental care and provide new avenues of research in this interesting

Future Directions

Why do some species care and others do not?

Even though reasonable understanding of the proximate causes behind the evolution of parental care exists, large-scale comparative analyses of the differences between lineages in which parental care has evolved and where care has not evolved are still lacking. For instance, since predation on the offspring is believed to be one of the key elements behind parental care, has parental care evolved more often in lineages with high levels of predation on offspring than with low levels of predation? Or is the evolution of parental care more linked to the habitat-type of a species such that only certain habitats provide adults the opportunity to protect a clutch of offspring? Or are both the level of predation and the habitat-type equally important for parental care to evolve? Considering the constant developments in the field of phylogenetic comparative biology and the development of robust phylogenies, these and many related questions could be interesting topics for future research. Especially the recent developments that allow for multivariate analyses of both discrete and continuous traits are promising as a means to disentangle the separate effects of many potentially different mechanisms.
field within evolutionary biology and behavioural ecology. See also: **Fitness; Life History Theory; Sexual Selection**

**Further Reading**


