

## When does it pay to be an absent parent?

Parental care can be thought of as any form of parental behaviour that appears likely to increase the overall fitness of the parent's offspring. This is a descriptive term and therefore does not carry any implications regarding the costs and benefits on energy expenditure and the parent's fitness, but instead focuses purely on the additive fitness for offspring (*Sheldon B, 2018*). Conflicts exist in many elements of parental care, between parents over relative provision of care, between siblings over relative demand of care, and between parents and offspring over supply and demand of care. It is clear that because of these differences in conflicts between species, as well as other confounding factors such as life-history constraints and ecological conditions, a vast array of differing parental care strategies have evolved. One of these strategies includes a distinct lack of parental care, either in the form of a total lack, whereby after birth neither parent makes any effort to protect or care for their offspring, or by the abandonment by one parent (*Davies NB et al, 2012*). The persistence of this strategy across the animal kingdom and the reason for its evolutionary origins will be assessed throughout this essay, thus bringing sense as to why it is beneficial for some individuals within species to be an absent parent.

### Single parent care

One form of absentee parenting is observed in the strategy of uniparental care, which is when the male or female parent deserts the offspring such that only one parent provides care. Ratios of female only care relative to male only and biparental care have been widely researched into, indicating that in mammals 95% of species exhibit female only care with no cases of male only care (*Clutton-Brock TH, 1991*), the ratio of fish genera with male only: biparental: female only care is 9:3:1 (*Reynolds JD et al, 2002*) and 8% of bird species exhibit female only care, compared 89.8% that display biparental or cooperative care and 1% showing male only care (*Cockburn A, 2006*). The imbalance of female only care in these clades of animals can be explained by their differences in reproductive biology.

Gametes desiccate when exposed to air, which evolutionarily has led to terrestrial animals adopting the strategy of internal fertilisation. This is significant because it means following copulation, the female will physically be left in possession of the zygote rendering it impossible for her to desert it while the male still can (*Dawkins R & Carlisle TR, 1976*). This biological phenomenon forces females into Trivers' "cruel bind" hypothesis, whereby the parent that is abandoned by its mate does not (or cannot) desert the offspring (*Trivers RL, 1972*). Therefore, one would expect high incidences of female only care (relative to male only care) in internally reproducing organisms, as demonstrated by the data that confirms these high frequencies in birds and mammals. In contrast, the high incidences of male only care reflect the fact that there is opportunity for the female to desert first due to the mechanism of external fertilisation. For example, in many fish species, both sexes spawn prior to fertilisation. Whichever partner spawns first is the one that is ahead and has the opportunity to desert, but there is a risk whereby spawning too early may lead to a situation where the partner is not ready to mate. Because sperm is lighter than eggs, they diffuse away faster and thus males generally risk more from premature spawning than females. This leads to a dynamic whereby females generally

spawn first thus forcing male fish into a cruel bind, further resulting in an increased incidence of male only care (*Dawkins R & Carlisle TR, 1976*).

While these dynamics might indicate why one parent might care over the other in certain species, it does not specify why uniparental care is beneficial in the first place. The benefits for being the absent parent in a pair are clear at face value. Following fertilisation, both parents have provided 50% of their genes into an embryo. This means both parents will receive an equal amount of benefit in the form of passing on their genetic information to future generations, independent of the post-copulation care mechanism, assuming that the offspring survive. Therefore, when it comes to parental care, both parents receive the benefit (the offspring), but only the caring parent pays the cost of energy expenditure. This is what results in a conflict of interest between males and females, asking which parent should provide the care (*Szentirmai I et al, 2007*).

The energy and time expenditure spent when caring for the offspring is significant because if the parent did not do this, they could be investing into new offspring (by reproducing more) thus giving them the opportunity to pass on more of their genes to future generations. This introduces a trade-off between investment into the current or future broods, first recognised by Williams in his paper on the costs of reproduction (*Williams GC, 1966*). The investment should optimise ‘lifetime reproductive success’, which can be thought of as the passing on of genes to offspring in an optimal way such that they too can pass on the genes to future generations (*Fisher RA, 1915*). An individual’s reproductive success can be maximised in different ways and underpins the existence of uniparental care systems.

In short, theory predicts that individuals should optimise entire lifetime reproductive success rather than just paternity or maternity following one reproductive attempt (*Griffin AS et al, 2013*). This can be applied in Hamilton’s Rule (*Hamilton WD, 1964*), which states that:

$$rb > c \quad \text{or} \quad rb - c > 0$$

In the case of uniparental care,  $r$  refers to the relatedness between the parent and the offspring,  $b$  is the fitness benefit of reproduction or care to the parent and  $c$  is the cost of care to future reproductive success. Because it can be assumed that  $r$  is fixed in these parent-offspring scenarios (because they will always share half their genes), parents should aim to optimise the value of  $b$  and decrease  $c$ . This brings understanding therefore as to why parents often aim to desert their mate and offspring such that they can mate again, observed in polygynous and polyandrous species, because they are decreasing the value of  $c$  without affecting  $r$  or  $b$  (assuming that the other mate provides care after desertion and the offspring survives).

Single parent care systems, whereby only maternal or paternal care is given to the offspring, has evolved due to the fitness benefit it confers to the parent that deserts the brood. Although it has proved to be a behavioural adaptive trait for a parent to abandon its mate and offspring, the sex it has evolved in across the animal kingdom is highly dependent on the species’ reproductive biology, specifically whether they undergo internal or external fertilisation.

## Biparental desertion

As well as solely maternal or paternal care, in some cases across the animal kingdom biparental desertion has evolved whereby offspring are not cared for at all. In these cases, two events may follow that still confer improved fitness. Either the biotic and abiotic factors acting on the offspring are sufficient such that they are able to survive and thus do not require parental care, or the desertion has evolved as a life history tactic whereby the conflicting interests between males and female act antagonistically to increase the reproductive success of the parent at hand (*Van Dijk RE et al, 2012*).

Examples of where both parents are absent and therefore no parental care is given is perhaps most obvious in teleosts, where 79% of families provide no care after spawning occurs (*Gross MR & Sargent RC, 1985*). This is made possible due to the environment in which the sex gametes are fertilised, because the fertilised eggs can be left in the aqueous environment and thus survive, although other factors such as increased risk of predation still arise without parental care. Despite this, abandonment of eggs is prominent in fishes as it often outweighs the costs that are associated with parental care such as decreased parental survival, increased time until next breeding attempt and reduced future fecundity (*Balshine S & Sloman KA, 2011*). Another strategy whereby it is possible for there to be no parental care is through brood parasitism. This is observed in cuckoos, whereby their eggs are laid in another species nest and thus the parents need not provide any parental care past this point provided the host species does. This has resulted in an evolutionary arms race between the cuckoo parasites and their hosts with respect to mimicry. Research has suggested that the begging call made by a cuckoo chick parasite mimics the sound that a brood of multiple reed warblers would make thus 'fooling' the host into the continuation of feeding (*Davies NB et al, 1998*). A final example of how no parental care can be achieved and yet offspring still survive is in the rare case whereby geothermal heat is used to rear young (*Cockburn A, 2006*). This occurs with the eggs of the superprecocial megapode species, whereby the young hatch in a supremely mature state and can often pursue prey and even fly on the same day as hatching (*Starck JM & Ricklefs RE, 1998*).

As stated, complete biparental desertion also occurs in cases where unusual life history sexual conflict dynamics occur between mates in certain species. This can be observed in penduline tits, where 30% of clutches are deserted by both parents. This takes place because male reproductive success (hereafter RS) increases with male desertion, mediated by the positive relationship between desertion and number of mates, number of eggs, number of sired hatchlings, and thus the RS over a breeding season. However, female desertion has a negative effect on male RS due to the relationship between female abandonment and total number of eggs in nests of the male and the number of hatchlings fathered by the focal male. On analysis of female RS, a study by Szentirmai et al showed prominent similarities with those of the males. Desertion by females increased the number of their mates and ultimately (through similar dynamics as those seen in males) their RS over the mating season. However, desertion by males reduced the females RS (*Szentirmai I et al, 2007*). This study demonstrated the first incidence whereby both males and females increase their own RS by deserting as well reducing their mate's RS, thus leading to behavioural

dynamics on a species level whereby biparental desertion of offspring can be observed on a significant level.

Biparental desertion is observed in the animal kingdom to a much lesser extent than that of the incidence of just one absent parent. As discussed, it exists via two different strategies. One whereby the deserted offspring are still capable of surviving despite a lack of care, and one whereby the abandoned brood is doomed to failure and will die, but despite this the total reproductive success of the parents are increased.

### Conclusion

Examples of differing parental care strategies across the animal kingdom suggest that being an absent parent can often be beneficial for the organism by increasing their reproductive success and thus fitness. The evolution of these absent parent strategies is highly interlinked with the physiologies of the organisms at hand. In most cases, it is likely that the strategy has evolved due to the specific physiologies that species have due to their environment, such as the importance of whether fertilisation occurs externally or internally. However, the dynamics of parental care that have evolved have no doubt been a part in shaping novel behaviours and physiologies of species, leading to further diversification that can be observed across the animal kingdom.

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