

Research Focus

It takes two to tango

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In most taxa, females are more likely than males to care for offspring. Why? Ever since Trivers' landmark work, the answer has been traced back to sexual differences in pre-mating reproductive investment (unequal gamete size or anisogamy). However, recent work shows that parental investment theory has inadvertently ignored a profoundly simple fact of life: every offspring has a mother and father. Taking this into account completely changes how we should think about sex differences in parental care.

In one of the best-known evolutionary game theory models to explain sex differences in parental care [1], both males and females have the option to desert rather than care for offspring, but the benefits of desertion differ between the sexes. A deserting female saves energy that enables her to lay more eggs per breeding attempt, whereas a deserting male has the opportunity to mate again with another female. Why should this usually produce female care? The conventional argument is that, for any female, reproduction is constrained by the demands of producing large, costly eggs, so she only gains a limited (small) increase in fitness if she decides not to care for her previous brood. By contrast, because sperm are small and cheaply produced, male fitness is only limited by access to receptive females. The fitness of a male can therefore increase indefinitely and linearly with the number of females with whom he mates [2]. This difference in potential reproductive rates means that the payoffs from deserting are usually larger for males than for females, so male care is less likely to evolve [3]. Although factors other than potential rates of reproduction can influence which sex is more likely to care (e.g. territorial male fish can care for several broods simultaneously without reducing their mating rate), the general rule of thumb is that 'the usually small investment of males [in endotherms] raises their potential reproductive rate so that any activity that constrains mating rate is likely to have heavy costs to males' [4].

This logic is taught in most introductory behavioural ecology courses. A similar argument is used to explain the evolution of anisogamy where, given initial variation in gamete size, disruptive selection favours the production of ever smaller gametes by one type of individual (males) because fitness increases more rapidly with investment in gamete number than in gamete size. The converse is true for producers of

larger gametes because these, when fertilized by small gametes, need high parental investment to survive [5]. The effect of an initial pre-mating asymmetry in parental investment on potential reproductive rates is also used to explain sexual selection. All else being equal, the sex with the smaller pre-mating reproductive investment (males) has a higher potential reproductive rate and competes for access to the more heavily investing sex (females), who can therefore afford to be more choosy. When all this is put together, the historical sequence of events is presented as follows. Isogamy is inherently unstable. The ensuing tradeoff between gamete number and size creates anisogamy. Because anisogamy affects potential rates of reproduction, it generates sexual differences in post-mating parental behaviour as males pay greater costs for caring. Differences in post-mating parental investment further elevate male competition for females, which again exaggerates sexual differences in mating behaviour. This chain of events therefore leads to the correlation between pre-mating and post-mating investment in offspring.

But can you spot the flaw in this argument? If you can't, take solace in the fact that it has gone largely unnoticed for over 20 years. In spite of recent work on the benefits of polyandry, it is probably true that male fitness depends more strongly on the number of matings than does female fitness. Even so, imagine that a naïve student asked you the following question: 'You just said males get higher benefits from deserting. But if females spend a lot of time caring, aren't there more males than females around willing to mate? So shouldn't a male have a much harder time finding a mate if he deserts than a female would? So how come his fitness gain can be higher?'

Good point, indeed. It is impossible for the total number of matings that males and females engage in to differ. It takes two to tango. (Popular surveys uncritically report that men have more sexual partners of the opposite sex than do women. These only show that humans can deny logic, not that they can defy it). The average male cannot achieve his higher potential without violating the principle that every offspring in diploid species has exactly one mother and one father. The irrefutable fact of identical average reproductive output per sex should have an enormous equalizing effect on male and female patterns of reproductive allocation. Fisher [6] used this seemingly inconsequential insight to explain the evolution of equal sex ratios, spawning a series of hugely successful models. When it

comes to parental care, however, our thinking has been somewhat careless.

Wade and Shuster [7] recently highlighted this problem by reanalyzing Maynard Smith's original model [1]. They formally show that it has an internal inconsistency because it violates the requirement of equal average male and female fitness. The problem is that deserting males gain 'extra' offspring by mating with females who materialize 'from nowhere' (i.e. they do not appear in calculations of female fitness). Males therefore have more total paternity than females produce offspring. This flaw can be corrected by explicitly stating where these offspring come from. For example, Wade and Schuster model a case in which deserting males have paternity in care-giving males broods, or mate with females who have deserted care-givers [7]. In general, when the additional paternity of a deserting male comes at a cost to the paternity of other males, models become self-consistent [8], and the logical flaws disappear.

The most exciting insight from Wade and Shuster's paper is that the initial direction of causality from parental care to sexual selection should be reversed. To understand why, it is instructive to glance at a delightfully simple but deeply insightful paper by Queller [9]. In this curiously neglected work, he noted that standard explanations for sexual differences in caring evaporate if we recognize that these costs must be measured in the currency of future offspring production. In spite of anisogamy, there is no inherent bias towards care by females if parents have identical future prospects of reproduction. On average they do, at least in populations with equal sex ratios. If one sex is rarer, however, then caring is more costly for that sex. One obvious way for males to become 'rarer' than females is when sexual selection generates nonrandom variance in mating success. Individuals that matter in the evolution of parental roles are those who 'qualify to mate' (*sensu* [10]): only they are in a position to be selected to provide parental care. The costs of caring differ among males if some, by virtue of being more attractive or aggressive, are consistently more successful than others in obtaining mates. Such males have a higher average reproductive rate than do females, which elevates their gains from deserting.

The second way in which sexual selection affects the evolution of caring is via the effect of sperm competition on certainty of parentage. With anisogamy, many small male gametes compete for access to eggs, be this because of female multiple mating or simultaneous sperm release in external fertilizers. Unless fertilization is internal and females are monogamous, males are less certain of their parentage in each zygote. But will this lead to less care? After all, males trade off current and future reproduction and low paternity could reduce benefits from both, without altering the balance [1]. Again, Queller [9] simply points out that low paternity does not imply low future reproduction for the male. Every future offspring has a father, and both legitimate and illegitimate progeny enter the equation for future reproductive success of males. Consequently, low paternity does not produce a sex bias in the costs of caring (reduction in future offspring production).

The only question we must then ask is whether the benefits of caring are smaller for males. For any given zygote, the benefits for a male are devalued by his lower average parentage, so we can safely conclude that males should care less.

To summarize, anisogamy does not generate a bias towards female parental care because males end up with a higher potential reproductive rate. It is actual rather than potential rates that count in evolution. Instead, anisogamy generates the conditions for sexual selection, as numerically abundant male gametes compete for access to rare female gametes. This lowers the confidence of males of paternity and, given direct male–male competition for access to females and/or female mate choice, creates an elite subset of males that are more eligible to mate. These two phenomena militate against the evolution of male care, relative to female care, because they reduce the benefits and increase the costs of caring, respectively. The arrow of causality therefore flies from sexual selection to post-mating sexual differences in parental care, rather than in the reverse direction.

Of course, this is a statement about the origins of sexual differences in care. From a contemporary perspective, we know there is feedback between levels of care and the intensity of sexual selection [11]. As females spend more time caring, the greater is the intensity of sexual selection on males to gain access to ever fewer receptive females. This seemingly unbreakable feedback loop should not, however, deceive us into forgetting that every journey starts somewhere, even if it ends up being a round trip.

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