THE EVOLUTION OF PARENTAL CARE

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ABSTRACT

Our understanding of parental care behavior can be significantly advanced through the application of Williams's Principle, *which states that reproduction has not only a benefit but also a cost to lifetime fitness. My laboratory has formalized Williams's Principle into the relative value theorem and found that its application to fishes, the taxa with the most diverse patterns of parental care, can help to explain which sex provides care and how much. In fishes, it is often the male that provides parental care, not because the male obtains greater benefits from this care, but probably because he pays fewer costs. Fish dynamically adjust their investment into parental care according to the number of offspring in their brood, past investment, genetic relatedness, and alternative mating opportunities, all of which affect the value of current offspring relative to potential future offspring. These results may also help us understand the joy and the challenges of parental care in humans.*

INTRODUCTION

PARENTAL CARE is an excellent example of a behavior that would seem to benefit the species. It promotes the survival and well-being of the next generation at a cost to the resources of the current generation, and the apparently sacrificial acts of individual parents compel our admiration. Human populations have entwined parental behavior into social, political, legal, and religious rules, and modern governments are often elected, or not, based on attitudes toward parenting and the family. Despite, or perhaps because of, this ardent ideology of parental care in human society, we remain largely ignorant of the biological basis for why we invest into raising our offspring.

In the 1960s, at a time when parental care was widely viewed among biologists to be an adaptation that benefits the species, George Williams authored *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (1966a), and "Natural Selection, the costs of reproduction, and a refinement of Lack's principle" (1966b). His explicit recognition of the cost of reproduction and gene-based fitness helped lay a foundation for current life history theory (e.g., Stearns 1992; Roff 2002). The significance of these concepts to scientists is reflected in how citation of these works continues to increase (Figure 1). Eventually, their importance may contribute to reshaping human social, political, and religious rules surrounding parental care.

I became interested in parental care behavior as a graduate student in the 1970s; for several decades, my students, colleagues, and I worked to understand its evolutionary properties. Our model organisms have been the fishes, the vertebrate group providing the greatest diversity of patterns in parental care. In this article, I wish to show the utility of Williams's Principle in answering two major questions about parental care: (1) "who cares?" (i.e., which sex is favored by natural selection to show parental care for the young?); and (2) "how much?" (i.e., what factors enter into
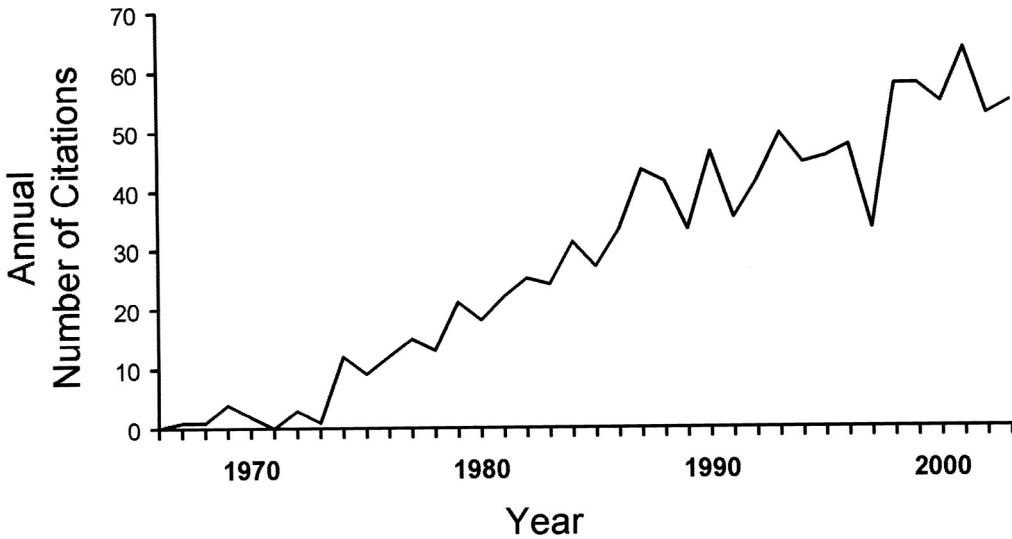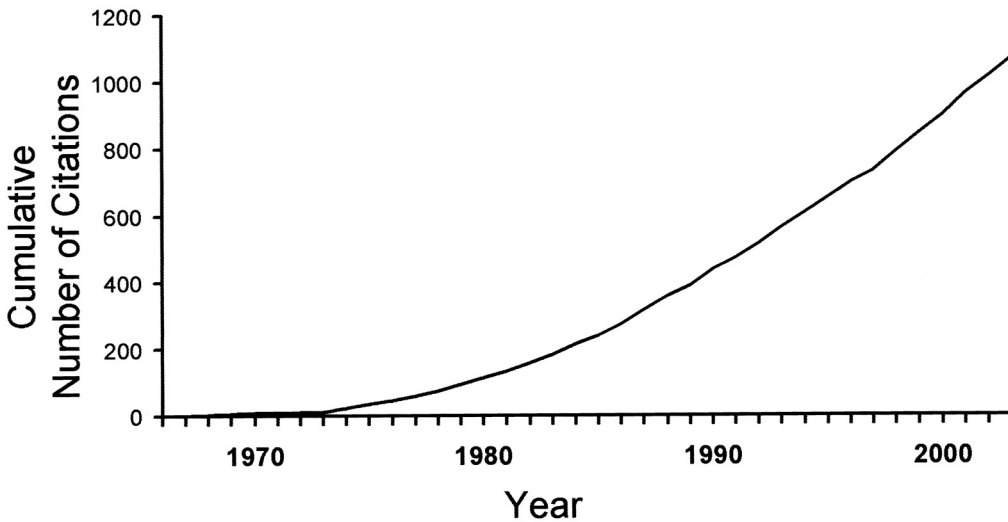
(a)

(b)

FIGURE 1.   CITATION FREQUENCY OVER TIME OF *NATURAL SELECTION, THE COSTS OF REPRODUCTION, AND A REFINEMENT OF LACK'S PRINCIPLE* (WILLIAMS 1966b)

  (a) Annual number of citations, and (b) cumulative number of citations, recorded by the Institute for Scientific Information (ISI) Web of Knowledge, from 1966 through 2003.

decision rules about the quantity of care to provide?). The question of which sex exhibits care helps us to understand the evolutionary origins of care, while the question of the amount of care helps us to understand its dynamic adjustment in quality. As most biol-

ogists know today, parental care behavior is not an adaptation to benefit the species; rather, parental care has evolved because it maximizes the selfish genetic interests of the parent. What is of interest to biologists today are the myriad life histories and sophisticated calculations that animals and plants have evolved to invest in the survival of their own genes into the future.

Williams's Principle

Williams's Principle was named as such when my postdoctoral fellow, Craig Sargent, who had recently obtained his PhD in George Williams's laboratory at the State University of New York, Stony Brook, and I realized that Williams's concept of life history tradeoffs and a cost of reproduction (Williams 1966a, 1966b) was central to bringing rigor into the study of parental care, which at the time was a relatively nonquantitative topic emerging from ethology (Gross and Sargent 1985; Sargent and Gross 1985, 1986). We were both interested in using fishes to study parental care and mating systems. Robert Trivers (1972) was implicitly using Williams's concepts and significantly advancing the field. At the University of Michigan, Bobbi Low was employing Williams's tradeoff theory to understand optimal mating and parental effort in relation to environmental uncertainty (Low 1978). Others were also interested in the notion of tradeoffs for understanding parental care (e.g., Pressley 1981; Carlisle 1982; Fagerstron 1982).

Modern life history theory recognizes that natural selection favors the evolution of behavior that will maximize lifetime reproductive success (LRS; the number of copies of genes that an individual leaves to future generations across its entire lifespan). Imagine a parent that has just produced a brood of offspring. Its remaining lifetime reproductive success can be divided into two components: that which is obtained through the present brood (P); and that which is obtained through all future broods (F). The number of current offspring, their genetic relatedness to the parent, and their survival—as well as the probability of future broods and their numbers, relatedness, and survival—cumula-

tively determine lifetime reproductive success. A further consideration is that the total effort that can be expended by an organism over its lifetime (E = 1) will be allocated into somatic effort (SE), which maintains the parent's own viability and growth, and reproductive effort (RE), which produces descendants. It follows that lifetime reproductive success is definable as success in the present (as a function of RE) and success in the future (as a function of SE), or LRS = P(RE) + F(SE). Williams's Principle is the recognition that investment into the present comes at the cost of investment into the future. Natural selection will therefore favor behaviors that maximize lifetime reproductive success subject to this constraint. In other words, reproduction has a cost (i.e., investment made into current progeny is traded off with investment made into future progeny), and natural selection will optimize the allocation of investment into the present relative to the future. From this, the relative value theorem, in which animals invest according to the value of their current brood relative to their own expected future reproduction (Coleman et al. 1985; Sargent and Gross 1985), can be derived. Continued investment into present progeny to increase offspring survivorship and fertility should be weighed against investments into expected future progeny through increased adult survivorship and breeding success. The optimal investment of RE occurs where the rates of return on investment into present and future reproduction are equal, as this will maximize lifetime reproductive success (Figure 2). Natural selection does not maximize reproductive success at any one time; it maximizes lifetime reproductive success by optimizing effort across time. These ideas are now well-summarized in parental care (e.g., Clutton-Brock 1991) and general life history texts (e.g., Stearns 1992; Roff 2002).

Who Cares?

There are significant taxonomic patterns in which one sex or the other will show care for the young (e.g., Reynolds et al. 2002). Among vertebrate species, for instance, mammals exhibit predominantly female-only care (found in about 90% of families) and a smat-
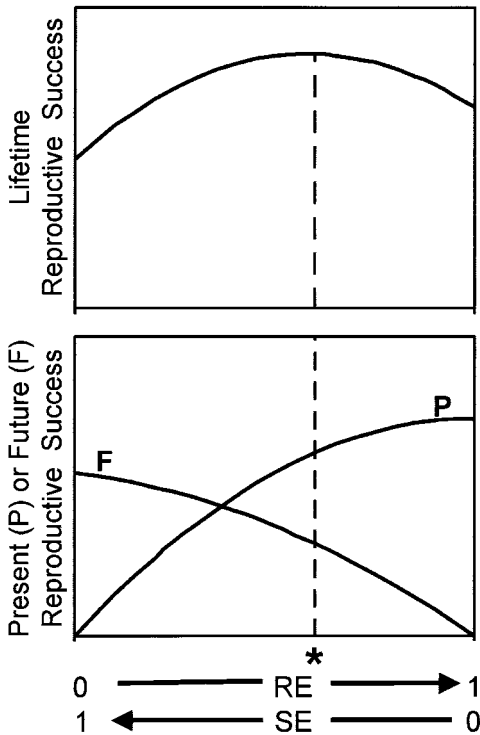
FIGURE 2. GRAPHICAL REPRESENTATION OF WILLIAMS'S PRINCIPLE.

The bottom panel is a hypothetical diagram of how reproductive success in the present and in the future may vary with investment into reproductive effort (RE) and somatic effort (SE), respectively. What is allocated into RE cannot be allocated into SE, therefore, there is a tradeoff in present and future reproductive success (i.e., a cost of reproduction). Natural selection will search for an optimal solution that maximizes lifetime reproductive success. In the top panel, lifetime reproductive success from present and future investment is maximized at the investments indicated by the asterisk (∗).

tering of biparental care (10%), but no cases of male-only care. Birds, on the other hand, are dominated by biparental care (about 90%), with female-only care being uncommon (8%), and male-only care being very rare (2%). In fishes, the majority of species provide no parental care at all for their young (Gross and Sargent 1985), but of those that do (about 20% of families), the majority exhibit male-only care (about 50%), followed by female-only care (30%), and biparental care (about 20%). Thus, while fishes have

evolved all forms of parental care, they are especially noteworthy for their male investment.

There has been considerable discussion about why fishes exhibit these alternative care states (e.g., Balshine and Earn 1998). In particular, why is there so much male-only care? The best explanation seems to come from the application of Williams's Principle: the consideration of both the costs and benefits of investing in parental care for a present brood relative to investment into future broods (Gross and Sargent 1985; Sargent and Gross 1986, 1993; Alcock 2001). In fish, female reproductive success (as measured by egg number) typically increases at an accelerating rate with adult body size, at least more so than it does in males. Male reproductive success tends to increase at a diminishing rate. Now imagine a mutant gene for showing parental care, and consider both the benefit to the parent's present reproductive success and the cost to its future reproductive success. Since most fish display indeterminate growth based on energy, the cost of present investment at the expense of future investment is likely to be exhibited in a feature such as body size; thus, a fish that does not show care for its young will be larger in the future than one that does. Because of the different relationships between body size and reproductive success, the mutant fish that shows care will suffer a greater future cost if it is female than if it is male (Figure 3a). Since most fish do not show strong sexual dimorphisms in morphological traits that can be used to provide parental care, and since most parental care by fishes consists of fanning eggs and guarding against predators, which both sexes can do, it is likely that either sex could provide the same degree of offspring survivorship per unit of parental effort (Figure 3b). If this is true, and if females pay the larger future costs, it is the male sex that derives the largest net benefit from providing parental care. At equilibrium, the average fitness of caregiving males and noncaring females will be equal (Charnov 1982). Thus, our modeling suggests that the predominance of male parental care in fishes evolved, not because the male sex obtained greater benefits from caregiving, but because males paid a lower future
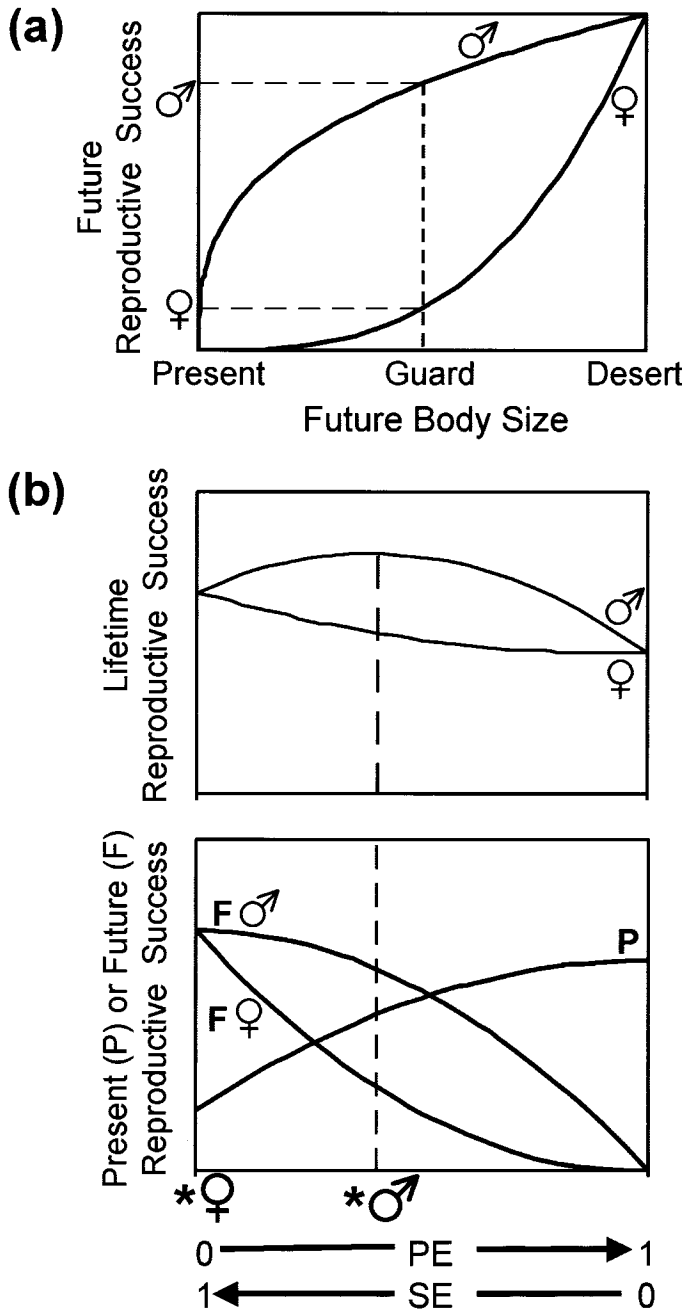
FIGURE 3.   GRAPHICAL REPRESENTATION OF SELECTION FOR MALE PARENTAL CARE.

(a) An accelerating reproductive success function for females and a diminishing function for males, with increasing body size, would result in a mutant guarding female (i.e., one who expends parental effort) forfeiting more future reproductive success than a mutant guarding male. (b) With equal present reproductive success from parental effort (PE), but dissimilar future reproductive success from somatic effort (SE) (e.g., by future growth), the lifetime reproductive success of females is maximized by deserting while for males it is maximized by guarding.

cost for the same benefits. This appreciation was obtained through consideration of Williams's Principle and the cost of reproduction; we simply realized that the costs are different for the two sexes, while the benefits in terms of increased offspring survival are the same. We would predict that the female sex provides parental care in species where the fitness functions are different from those shown in Figure 3. For example, female Pacific salmon are semelparous, but males can breed multiply in a season. Thus, there would be no cost of parental care to future breeding opportunities for females, but there would be a cost for males. In these fish, females have evolved to defend the embryos in their nests until death, while males chase after other mating opportunities (van den Berghe and Gross 1989). Species will evolve biparental care when both sexes obtain maximum lifetime reproductive success through care (i.e., local maxima in the LRS functions), and neither sex will show care when the benefit of care does not exceed the loss to future reproductive success. These are all testable predictions that are an active part of current parental care research (e.g., Balshine et al. 2002).

How Much Care?

When studying a wild population, one finds a remarkable amount of variation in the parental care provided by parents. Some seem ready to fight to the death in the protection of young while others are more indifferent and may desert the nest rather than face a potential predator. It has become clear that parental care is not an all-or-none behavior; rather, it is dynamically adjusted to individual circumstances. What, then, are the key factors that underlie the parental investment decisions of adults? Using our model for present and future investment tradeoffs and the decision rule to invest according to the value of the present brood relative to the value of future broods, I will briefly describe four major factors that influence the amount of parental care that is provided: brood size, past investment, genetic relatedness, and future mating opportunities.

BROOD SIZE

The number of offspring in a brood receiving care is likely to be a strong predictor of how much parental investment is provided because of its direct relationship to brood value. Many male fish that show care, for example, build nests, attract females, and then fan the eggs and guard both eggs and fry from predators. Nests will vary in number of eggs for many reasons, including the number of females that were attracted and the number of offspring lost to predators. We would therefore expect male fish to evaluate the number of offspring in their nests and adjust their parental investment accordingly, relative to their expectations for future nesting events. We tested this prediction by manipulating the egg numbers in nests of bluegill sunfish (*Lepomis macrochirus*) (Coleman et al. 1985), a species where males can make several nests within a season and can survive to breed for multiple years. When examined for willingness to defend the brood from a dummy predator, the defense score of males with experimentally reduced broods was less than that of control males. This showed that male bluegill sunfish are not static in their parental investment, but instead incorporate the value of the present brood in their investment decision. Other researchers have shown similar findings (e.g., Galvani and Coleman 1998; Amundsen 2003).

PAST INVESTMENT

Imagine that, for a given number of young, some fish have expended a great deal of energy while others have not. This might be because the former had a much larger clutch, recently reduced by predators to the same size of clutch as the latter. We now have two groups of parents with equal clutch size, but one group has made greater past expenditures than the other. Many researchers found that the former group of parents would work harder at defending their current clutch than would the latter, even though both sets of parents now had clutches of the same size (see Sargent and Gross 1985; Coleman and Gross 1991). The implication drawn was that these parents were working to minimize wastage of past investment when they should be working

to maximize future gains. The apparent finding that animals were investing improperly stirred up considerable controversy, known as the "Concorde Fallacy" (Dawkins and Carlisle 1976; Curio 1987). We showed, however, that the resolution to this perceived fallacy was to be found in Williams's Principle and the relative value theorem (Sargent and Gross 1985; Coleman and Gross 1991). The relative value of a current brood increases whenever future opportunity is decreased, such as by the independent expenditure of energy that is no longer available for the future. In this situation, the variation that one finds in parental investment for the same brood size, therefore, has an explanation in the future opportunities of parents as a consequence of their past investment histories.

GENETIC RELATEDNESS

Genetic relatedness between adults and young in their care can vary considerably in nature due to various forms of cuckoldry. When I first reported cuckoldry in sunfishes (Gross 1979), it was to a disbelieving community: how could such alternative tactics for parasitising parental care exist? But we now know that cuckoldry is widespread and probably the norm in parental care systems (e.g., Alcock 2001). The first challenge in understanding whether genetic relatedness was relevant to parental care was to show its role in the evolutionary origin of care from a no-care state (e.g., Maynard Smith 1977; Werren et al. 1980; Gross and Shine 1981). After this emerged the question as to whether parents assess genetic relatedness and incorporate this information into their ongoing investment decisions. We recently provided a demonstration that male bluegill sunfish that have been cuckolded will either increase or decrease their parental investment in response to changing information on paternity during brood development (Neff and Gross 2001; Neff 2003). When parental males have detected, perhaps through odor cues, that their paternity has been reduced by cuckoldry, they adaptively lower their level of parental care; when they detect that their paternity is higher than previously assessed, they adaptively raise their level of parental

care. This dynamic adjustment of care during brood rearing strongly confirms the importance of genetic relatedness in parental investment decisions.

MATING OPPORTUNITIES

An important factor in determining future investment returns is the number of potential mating opportunities, especially for males. Simply placing the biparental cichlid *Herotilapia multispinosa* into ponds at three adult sex ratios and recording male desertion rates was one of the first documentations that future opportunities to remate affect parental investment decisions. Keenleyside (1983) found male desertion to increase from 12% to 22% to 51% as the number of females in their environment increased from 5:7, 6:6, and 7:5 in female to male sex ratio. Males increasingly deserted their mates and the young in their care as the opportunity to remate increased in their environment. A more sophisticated study and analysis was later conducted by Balshine-Earn and Earn (1998).

HUMAN PARENTAL CARE

Most human parents will experience both the joy and the suffering that is parental investment. While the sacrifice made by parents is readily evident, from an evolutionary perspective, this sacrifice is no more altruistic than breathing. Like other species, human parental investment behavior originated by natural selection to better project the parent's genes into the future. Therefore, humans have been molded, as have fish, by the laws of Williams's Principle. Given this evolutionary history, humans are expected to calculate optimal investments in their offspring, incorporating those factors that influence the net value of care. This helps to explain why researchers find human parental care to vary with the relative value of current offspring (e.g., Lycett and Dunbar 1999), their genetic relatedness to the parent (e.g., Daly and Wilson 1999), and additional adult mating opportunities (e.g., Gangestad and Simpson 2000).

Can human society adequately address such issues as parenthood, birth control, abortion, adoption, postpartum depression, child abuse,

and child neglect, to name but a few, without understanding their biological causes? In this light, the full contribution of Williams's Principle to human society remains to be seen.

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