

The Evolution of Parental Care in the Context of Sexual Selection: A Critical Reassessment of Parental Investment Theory

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ABSTRACT: Males and females are often defined by differences in their energetic investment in gametes. In most sexual species, females produce few large ova, whereas males produce many tiny sperm. This difference in initial parental investment is presumed to exert a fundamental influence on sex differences in mating and parental behavior, resulting in a taxonomic bias toward parental care in females and away from parental care in males. In this article, we reexamine the logic of this argument as well as the evolutionarily stable strategy (ESS) theory often used to substantiate it. We show that the classic ESS model, which contrasts parental care with offspring desertion, violates the necessary relationship between mean male and female fitness. When the constraint of equal male and female mean fitness is correctly incorporated into the ESS model, its results are congruent with those of evolutionary genetic theory for the evolution of genes with direct and indirect effects. Male parental care evolves whenever half the magnitude of the indirect effect of paternal care on offspring viability exceeds the direct effect of additional mating success gained by desertion. When the converse is true, desertion invades and spreads. In the absence of a genetic correlation between the sexes, the evolution of paternal care is independent of maternal care. Theories based on sex differences in gametic investment make no such specific predictions. We discuss whether inferences about the evolution of sex differences in parental care can hold if the ESS theory on which they are based contains internal contradictions.

Keywords: parental care, offspring desertion, sex ratio, anisogamy, sexual selection.

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The evolution of parental care of offspring from a “non-caregiving” ancestral state is generally seen to involve an essential fitness “trade-off” (Clutton-Brock 1989, 1991). This trade-off is presumed to exist between the immediate fitness gain parents receive from enhancing the survival of their current offspring and the delayed fitness parents gain from future reproduction, the former coming at the expense of the latter. According to this hypothesis, males and females experience this trade-off in different ways, resulting in a taxonomic bias toward female parental care and away from male parental care. The predicted taxonomic bias is consistent with Bateman’s (1948, p. 365) arguments for a sex difference in “the capacity for rearing young.” These arguments are based on anisogamy, that is, the tendency of males to produce many small sperm and for females to produce fewer large ova: “The fertility of the female is limited by egg production which causes a severe strain on their nutrition. In mammals the corresponding limiting factors are uterine nutrition and milk production, which together may be termed the capacity for rearing young. In the male, however, fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him” (Bateman 1948, p. 365).

Bateman’s original arguments were extended by Trivers (1972) and Parker et al. (1972) and formalized in an evolutionarily stable strategy (ESS) model by Maynard Smith (1977). The resulting “parental investment theory” has become the foundation of most current research in sexual selection and mating system evolution (Trivers 1972; Bradbury and Veherencamp 1977; Emlen and Oring 1977; Borgia 1979; Wickler and Seibt 1981; Wittenberger 1981; Thornhill and Alcock 1983; Bradbury 1985; Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Arnold and Duvall 1994; Parker and Simmons 1996; Reynolds 1996).

Parental investment theory underlies explanations for the evolution of sex differences in the pattern of parental care. The fitness gain, which might accrue to a male from

his caring for existing young and incrementing their viability, is viewed as much smaller than his potential fitness gain from additional matings. In addition, in species with internal fertilization, certainty of offspring parentage tends to be greater for females than for males (Trivers 1972; Alexander and Borgia 1979; Clutton-Brock 1991; Svensson et al. 1998). Uncertain paternity thus appears to diminish the potential fitness gain to caregiving males below that of females. In species with external fertilization, such as fish and amphibians, gametic proximity has been proposed to influence parental care, wherein the sex closest to the eggs at fertilization subsequently cares for them (Trivers 1972; Williams 1975; Dawkins and Carlisle 1976; but see Gross and Shine 1981; Beck 1998; and Tallamy 2001 for contradictory evidence). According to this hypothesis, the parent nearest to the eggs is more often the male, who is faced with the “cruel bind” (Trivers 1972, p. 148) of caring for the young at hand and forgoing additional matings or squandering investment in current young for future mating success.

Additional fitness considerations have been used to elaborate the basic argument for a sex difference in post-fertilization offspring investment. For example, one hypothesis suggests that male parental care provides females a direct fitness benefit via mate choice as well as an indirect, “good genes” benefit—the increased number of grandchildren caregiving sons may produce (Møller and Thornhill 1998).

In this article, we reexamine the logic of these arguments as well as the ESS theory often used to substantiate them (Maynard Smith 1977; Alexander 1996). We show that constraints that necessarily connect the mean male and female fitness (Fisher 1930; Wade 1979, 1995) are violated in this ESS model, which contrasts parental care with offspring desertion. When the constraint of equal male and female mean fitness is correctly incorporated into the ESS model, its results are congruent with those of evolutionary genetic theory that govern the evolution of genes with differing direct and sex-limited parental effects on fitness (Cheverud 1984; Wade 1987, 2001; Kirkpatrick and Lande 1989). Moreover, the specific predictions of parental investment theory regarding sex differences in initial gametic investment and parental care disappear.

The ESS Model of Parental Care

In ESS models, as in population genetic theory, a population can be stably polymorphic for two (or more) strategies or alleles at equilibrium, as long as the strategies or alleles have equal marginal fitnesses. Stable within-sex polymorphisms also require the equilibration of fitnesses as well as the constraint that the average fitness of males must equal that of females, multiplied by the sex ratio, R .

Thus, the fitness matrix of an ESS model of sex differences in reproductive strategies must also be subject to the constraint that the average fitness for males equals that for females at all times and not just at the final equilibrium.

The payoff matrix for the evolution of parental care (Maynard Smith 1977; Alexander 1996) assumes different fitness consequences for males and females as a result of caring for or deserting offspring (table 1). The fitness entries for females in the matrix (table 1) assume that there are two kinds of females: caring females, who lay W_c eggs, and deserting females, who lay W_d eggs. Let the frequency of caring females be f_c and that of deserting females be $1 - f_c$, or f_d . Because deserting females save energy by not providing parental care, they can lay additional eggs. Hence, it is also assumed that $W_c < W_d$. Because maternal care increases offspring viability, it is assumed that offspring survivorship for caregiving females, S_c , exceeds that of deserting females, S_d , that is, that $S_d < S_c$. Total fitness is the product of the number of eggs laid multiplied by egg survivorship.

With these assumptions about the two fitness components, the female strategy with the highest total fitness, $W_c S_c$ or $W_d S_d$, will come to predominate in the population. Deserting females will replace or prevent invasion by caregiving females whenever $W_d S_d$ exceeds $W_c S_c$, while the converse obtains when $W_c S_c$ exceeds $W_d S_d$. Taken together, the negative covariance between egg number and survival represents a fitness trade-off for females between investment in present (S_c) and future (W_d) reproduction. In this sense, caring for present offspring imposes on females an “opportunity cost” in the form of sacrificed future reproduction. A polymorphic population with caregiving and deserting females can exist when the average fitnesses of the two strategies are equal (i.e., $W_c S_c = W_d S_d$). Because each of these fitness payoffs to reproducing females is framed in terms of total surviving offspring within the same generation, they are comparable.

This straightforward analysis becomes more complicated when offspring survivorship depends on the parental

Table 1: The payoff matrix to males and females in the ESS model of the evolution of parental care

Males	Females	
	Cares for young	Deserts
Cares for young:		
Female fitness	$W_c V_2$	$W_d V_1$
Male fitness	$W_c V_2$	$W_d V_1$
Deserts:		
Female fitness	$W_c V_1$	$W_d V_0$
Male fitness	$W_c V_1(1 + p)$	$W_d V_0(1 + p)$

Sources: Maynard Smith 1977; Clutton-Brock 1991, table 7.1, p. 105; see also Alexander 1996, table 5.1, p. 135.

behavior of males as well as females. The fitness matrix of table 1 assumes that there are two kinds of males: caregiving males, who mate once and increase offspring survivorship by delivering care, and deserting males, who do not provide care and enjoy the fitness benefit of additional matings with probability p . With caregiving by both sexes, offspring survival can take three possible values, V_0 , V_1 , or V_2 , corresponding to the number of parents providing care, 0, 1, or 2, respectively. Furthermore, because more care is better than less care, it is assumed that $V_0 < V_1 < V_2$. (This formulation implicitly assumes that the quality of male caregiving is equivalent to that of females. More complicated possibilities, with sex differences in care quality, have been explored in other models.)

Despite these additional considerations, S_d tends to be lower than S_c because the offspring viability of caring females consists of an average of the larger values, V_2 and V_1 , whereas, for the noncaring, deserting females, offspring viability is the average of the two smaller values, V_1 and V_0 . Nonrandom mating by females, contingent on evaluating the likelihood of male caring or deserting, can greatly complicate calculating this fitness average, as can the hypothesis that male deception may confound female assessment of mate caregiving quality. We will not consider these additions to the standard model (table 1) for reasons we will describe below.

Similar to the logic for females, the evolution of the alternative male strategies depends on the relative magnitudes of the increments to male fitness that derive from caregiving versus pursuing additional matings. When the additional survival of nurtured present offspring, S_c , exceeds the gain of additional copulations (calculated as mating probability p times average female fecundity), caregiving, monogamous males will enjoy higher fitness than deserting, polygamous males. When the converse is true, the male strategy of desertion and polygamy will spread throughout the population (unless limited in some frequency-dependent manner). Similar to the case for females, the calculation of the average fitness effect of a given strategy can be complicated by nonrandom mating, especially that based on male caregiving potential or the appearance thereof.

In the standard analysis of this fitness matrix (e.g., Clutton-Brock 1991), there are four possible outcomes, depending on the conditions under which the game is played. They are as follows: both sexes desert; males desert, females care; males care, females desert; and both sexes care. The four outcomes of this single model blanket the range of possibilities observed in nature, so it is often assumed that the explanation for taxonomic variation in the manifestation of parental care is determined by taxonomic variation in the ecologies underlying the relative fitness increments and decrements. For example,

it is frequently argued (somewhat circularly) that additional matings must confer a greater increment to male fitness than could occur through enhanced offspring survival because males of so many species do not provide care. Similarly, fitness gain through additional matings is a strategy available to males but not to females as a result of the fundamental asymmetry of anisogamy. The existence of all four possible outcomes from the model is itself taken as evidence in support of the analysis. Thus, the model is not tested but rather confirmed by observation. Clearly there are other evolutionary considerations, such as the coevolution of male and female behaviors noted by Clutton-Brock (1991), that lie beyond the scope of this ESS model.

As we explain in the next section, we believe that this ESS model is fundamentally flawed and that when it is corrected the results will be congruent with standard evolutionary theory. There are, however, important differences between the interpretation of the results from evolutionary genetic theory and the ESS model. In particular, the fitness gain from additional matings is a direct contribution to male fitness, while the gain from enhanced offspring viability is indirect. Thus, the latter must be weighted by a factor of 1/2 when assessing the relative costs and benefits of caregiving versus additional matings.

Flaws in the ESS Model

We take table 1 as our starting point to illustrate the flaws of the ESS model. With two strategies for each sex, there are at least four different kinds of matings. Four is the minimum number of possible outcomes because deserting males are presumed to remate in an unspecified manner. That is, there is no explicit model for pairing deserting males with either kind of female, nor is the source of the "extra" females acquired by deserting males discussed. Let the frequency of the four mating types be given by $G_{c,c}$, $G_{c,d}$, $G_{d,c}$, and $G_{d,d}$, where the subscripts denote whether an individual cares (c) or deserts (d), with females listed first and males second. Thus, $G_{d,c}$ is the frequency with which deserting females mate with caregiving males. The sum of these four mating-type frequencies must equal 1. We will not make any further assumptions about the mating-type frequency distribution, so our conclusions apply to random mating or any pattern of nonrandom mating.

We weight the sex-specific fitnesses from table 1 by mating-type frequencies in order to calculate the average fitness of males, W_{males} , and females, W_{females} . We find that mean female fitness equals

$$W_{\text{females}} = G_{c,c}(W_c V_2) + G_{c,d}(W_c V_1) + G_{d,c}(W_d V_1) + G_{d,d}(W_d V_0). \quad (1)$$

Table 2: The adjusted payoff matrix to males and females in the ESS model of the evolution of parental care

Males	Females	
	Cares	Deserts
Cares:		
Female fitness	$W_c V_2$	$W_d V_1$
Male fitness	$W_c V_2(1 - pm_d)$	$W_d V_1(1 - pm_d)$
Deserts:		
Female fitness	$W_c V_1$	$W_d V_0$
Male fitness:		
Fails to remate	$W_c V_1$	$W_d V_0$
Remates	$W_c V_1 + (G_{c,c}W_c V_2 + G_{d,c}W_d V_1)$	$W_d V_0 + (G_{c,c}W_c V_2 + G_{d,c}W_d V_1)$

Sources: Maynard Smith 1977; Clutton-Brock 1991, table 7.1, p. 105.

However, because table 1 does not specify what happens to the initial mating-type frequencies or to female fitness when some males desert and find new mates, the model is incomplete. Implicit in the fitness matrix is the assumption that additional matings by deserting males do not change female fitness in any way. This implication is evident in two features of table 1: first, no entries are included for remating females, and second, the payoffs for remating males are given simply as p times the fitness of caring or deserting females, $W_c V_1$ or $W_d V_0$, respectively.

Mean male fitness is more problematic than that of females. From the mating-type frequency distribution and the fitness entries in table 1, we find that

$$W_{\text{males}} = G_{c,c}(W_c V_2) + G_{c,d}[W_c V_1(1 + p)] + G_{d,c}(W_d V_1) + G_{d,d}[W_d V_0(1 + p)]. \quad (2)$$

Comparing equations (1) and (2), we see that there is a sex difference in mean fitness, ΔW , equal to

$$\Delta W = W_{\text{males}} - W_{\text{females}} = p[G_{c,d}(W_c V_1) + G_{d,d}(W_d V_0)]. \quad (3)$$

Since all terms on the right-hand side of equation (3) are positive, mean male fitness must exceed mean female fitness, $W_{\text{males}} > W_{\text{females}}$. Because the mean fitness of males is related to that of females via the sex ratio,

$$W_{\text{males}} = (R)(W_{\text{females}}), \quad (4)$$

this implies that R must exceed 1.0. And yet whenever the sex ratio, R , is unity, this is not possible. Hence, when R is 1, the fitness matrix of table 1 can be reconciled with standard evolutionary theory only if one of two conditions apply. Either p equals 0 or the frequency of matings involving deserting males ($G_{c,d} + G_{d,d}$) is 0. That is, either deserting males gain no additional matings or there are

no deserting males. If the sex ratio, R , is not 1, then equation (3) implies that females must always be more abundant than males and that some females postpone reproduction in order to mate with deserting males. In each of these cases, the ESS analysis of the strategies of deserting versus caregiving is undermined. Although the fitness matrix in table 1 awards a higher fitness to males than to females, no such sex ratio restriction has been placed on the analysis of this model, neither in discussions in the literature nor in its application to various taxa. We are left with the question: Are the inferences about the evolution of sex differences in parental care true if the theory on which they are based contains internal contradictions? The taxonomic patterns, such as those reviewed in Clutton-Brock (1991), exist, but the explanation for them is founded on a flawed (or at least incomplete) theoretical model.

Correcting the Flaws

The entries in table 1 can be modified to eliminate the flaw in a way consistent with both the fitness trade-offs that motivated the original entries and standard evolutionary theory. However, to effect such modifications and make the fitness matrix internally consistent, we are faced with more than one option. Here, we address the simplest case, wherein deserting males, whose frequency is $m_d (= G_{c,d} + G_{d,d})$, take a fraction of matings away from caregiving males (table 2, row labeled "Male fitness" under "Cares"). This is consistent with Darwin's fundamental idea that "the practice of polygamy leads to the same results as would follow from an actual inequality in the number of the sexes; for if each [successful] male secures two or more females, many males cannot pair" (1874, p. 212).

Differently put, females or their ova are a limited resource. If desertion is a male strategy whose fitness payoff derives from additional matings, then these additional

matings must come at the expense of matings by other males. Here, we assume that these additional matings come at the expense of males practicing the alternative strategy of providing offspring care, regardless of whether the offspring have a caregiving or deserting mother.

Note that we must now keep track of two kinds of deserting males, those who are successful and those who are unsuccessful at remating. Consistent with table 1, we assume that a fraction, p , of deserting males is successful at remating. Unlike table 1, we specify the source of the additional matings by deserting males who are successful at remating. In table 2, the fitness gains to deserting, remating males are accounted for as decrements to the fitness of caregiving males, that is, reductions in the fitness of $G_{c,c}$ and $G_{d,c}$ family types. Because it might be more reasonable that the extra matings accruing to deserting males involve deserting females rather than caregiving females, we also explore this possibility in table 3. Neither change (table 2 or 3) involves changes in female fecundity fitness or offspring survivorship dependent on female care. That is, additional matings with deserting males do not change either the number of eggs laid by deserting females or the contribution of females to the viability of their offspring. These extra matings change only the distribution of offspring among male types, removing some of the offspring of deserted, caregiving males and awarding them to deserting males. Unlike the original ESS model, this exchange of fitness between male strategies does not create a sex difference in mean fitness (table 1).

How do our adjustments of the fitness matrix affect our understanding of the evolution of parental care? Because the analyses of tables 2 and 3 and the conclusions drawn are similar, we begin with the simpler case of table 3, where the additional matings of remating, deserting males occur exclusively with deserting females. We follow the same fitness logic as that employed in the analysis of the ESS model and compare the mean fitness of deserting males with that of caregiving males. Substituting values from table 3, we find that the mean fitness of caregiving males, $W_{c,males}$, is less than that of deserting males, $W_{d,males}$, when

$$W_d V_1 (1 - p) < W_d V_0 + p G_c W_d V_1, \quad (5a)$$

or

$$V_1 (1 - p) < V_0 + p G_c V_1. \quad (5b)$$

Setting V_1 equal to 1.0 and V_0 equal to $(1 - s)$, we can reduce expression (5b) to

$$1 - p < 1 - s + p G_c. \quad (6)$$

Table 3: The adjusted payoff matrix to males and females in the ESS model of the evolution of parental care

Males	Females	
	Cares	Deserts
Cares:		
Female fitness	$W_c V_2$	$W_d V_1$
Male fitness	$W_c V_2$	$W_d V_1 (1 - p)$
Deserts:		
Female fitness	$W_c V_1$	$W_d V_0$
Male fitness:		
Fails to remate	$W_c V_1$	$W_d V_0$
Remates	$W_c V_1 + (G_{d,c} W_d V_1)$	$W_d V_0 + (G_{d,c} W_d V_1)$

Sources: Maynard Smith 1977; Clutton-Brock 1991, table 7.1, p. 105.

If we are modeling invasion of the deserting strategy, then G_c is approximately equal to 1, and we find that

$$1 - p < 1 - s + p. \quad (7)$$

This reduces further to the condition

$$\frac{s}{2} < p. \quad (8)$$

The condition represented in equation (8) is identical to that obtained from evolutionary genetic theory, which contrasts the evolution of indirect, parental effects with direct fitness effects (Wade 1998, 2001; Wolf and Wade 2001). Indirect parental effects, like caring for offspring, are discounted by a factor of 1/2 relative to direct effects, like obtaining additional mates. From elementary population genetic theory, the equation governing the evolution of an allele with a direct additive effect on fitness, s_d , is

$$\Delta p = \frac{s_d p q}{W}, \quad (9)$$

while the analogous equation (e.g., Wade 2001) for a sex-limited, parental effect on offspring viability, s_p , of the same magnitude ($s_d = s_p$) is

$$\Delta p = \frac{s_p p q}{2W}. \quad (10)$$

The rate of evolution of the indirect, parental effect is half that of a direct effect because it represents among-family selection (Cheverud 1984; Cheverud and Moore 1984; Wade 1998, 2001). Differently put, the evolution of an allele with a maternal or a paternal effect on offspring viability fitness of s depends on the value of $s/2$ because the allele is expressed in only half the individuals in the population (Wade 1998, 2001). The evolution of an allele

with antagonistic pleiotropy of direct and indirect effects (i.e., $s_d < 0 < s_p$ or $s_d > 0 > s_p$) is governed by

$$\Delta p = \frac{(s_d + s_p/2)pq}{W}. \quad (11)$$

The condition represented in equation (8) states that the deserting male strategy will invade and spread whenever half the magnitude of the indirect effect of paternal caregiving on offspring viability, $s/2$, is less than the direct effect of additional mating success, p , gained by desertion. When the converse is true, the male caregiving strategy will invade and spread. This is the same condition as would derive from equation (11) if the direct (s_d) and indirect (s_p) effects were of opposite sign, indicating that a positive indirect effect on offspring viability came at the expense of a direct effect on fertility.

We can contrast this condition with that of the Maynard Smith (1977) model (table 1), as reported for the case where females always desert (in Clutton-Brock 1991), $P_0(1 + p) < P_1$. Substituting V_0 for P_0 and V_1 for P_1 , we find that the flawed model predicts that males should desert when

$$\frac{s}{1-s} < p. \quad (12)$$

The correct condition, equation (8), is always easier to satisfy than this condition derived from the incorrect model represented in equation (12) because, for all values of s , $s/2 < s/(1-s)$. This result is not an endorsement of the widely held notion that, since males "have to invest" in mate acquisition, they "must invest" fewer resources in parental care (e.g., Parker 1979). Ultimately, the fraction of males successful at obtaining additional mates, p , cannot be more than $1/2$, since for every male successful at taking a mate away from another male there must be a mated male that loses a mate. Thus, a positive effect of paternal care ($0 < s < 1$) may suffice to make equation (8) true.

When the extra matings involve caregiving females (table 2), then we need more information than can be gleaned from the classic game theory model. The central issue is whether caring females lay more eggs and increase W_c to W_d if, although caring for a first clutch, they mate again with a deserting male. If not, then female fecundity fitness does not change. If the female has already been deserted, then these matings also do not affect the distribution of offspring among male types; offspring are simply being exchanged between deserting males. The problem arises because the classic model has only two female fitnesses, W_c and W_d , but six kinds of females, caring or deserting factorially combined with three possible pairs of males. The central question is this: Does offspring viability change

when a caring female mates again with a deserting male? That is, Does the fitness of a female change with the behavior of her mate(s)? It could, for example, if she was mated to a caregiving male and he subsequently withdrew or reduced his level of care. If so, then mean female fitness is reduced below that used in equations (5a) and (5b). If not, then no changes are necessary. The classic model does not address possibilities such as these. In summary, if male mating behavior simply exchanges offspring among males (within or between male types) without changing either female fecundity or offspring survival, then equation (8) holds. However, if cuckolded, caregiving males reduce or withdraw care, then mean female fitness must be lowered.

Discussion

Parental investment theory typically assumes that anisogamy is sufficient to generate the reproductive competition that constitutes sexual selection, whenever the number of small gametes produced by males exceeds the number necessary to fertilize the ova of a single female (Trivers 1972; but see Parker et al. 1972). Sexual selection resulting from the variance in mate numbers of the sex producing small gametes does not occur in asexual populations (Agrawal 2001). Parental investment theory further predicts that gamete dimorphism initiates sexual selection because the few large ova produced by females are a limited resource for which the microgametes produced by males must compete (Parker et al. 1972). Thus, males are expected to be more competitive in mate acquisition, less discriminating in mate choice, and less parental toward offspring than females, as a result of anisogamy (Alexander and Borgia 1979; Thornhill and Alcock 1983; Kvarnemo and Ahnesjö 1996; Waage 1997). As Trivers states: "The single most important difference between the sexes is the difference in their investment in offspring. The general rule is this: females do all of the investing; males do none of it" (Trivers 1972, p. 207).

Many of the same arguments that apply to parental investment in gametes also are applied in the discussion of postfertilization offspring care. Despite their popularity in recent years, these approaches to the analysis of sexual selection are inadequate for understanding the evolution of mating systems. The confounding of multiple investments, in gametes, in offspring sex ratio, and in parental care, clouds rather than clarifies theoretical issues of the sex difference in the strength of selection, the origins of anisogamy, and the evolution of parental care. Ratios of gametic investment do not measure either the sex difference in the strength of selection (Shuster and Wade 2003) or the intensity of sexual selection (Wade 1979; Wade and Arnold 1980). Anisogamy may permit sexual selection and competition for mates, but it does not predict the strength

or direction of selection because it is not proportional to the variance in relative fitness of either sex. Measuring sex-specific selection requires estimates of relative fitness before and after each episode of selection for each sex (Crow 1958, 1962).

As we have shown above, an additional difficulty with the parental investment approach to the study of parental care is that it combines direct and indirect effects on male fitness in an unweighted manner. There is little doubt that males of many species invest smaller amounts of energy than females in terms of gametic mass or parental care. However, the fitness trade-off between paternal offspring care and male mating success has not been properly incorporated into behavioral models in at least two ways. First, such models fail to recognize the inherent difference between indirect effects on offspring viability, like parental care, and direct effects on individual fitness, like male mating success. Because of these differences, increments to fitness resulting from indirect effects must be weighted differently than increments to fitness based on direct effects. Indeed, as shown in Wade (2001), the weightings differ between haplo-diploid and diplo-diploid organisms, making it easier to evolve parental effects in the former than in the latter.

Second, mating success is competition for limited reproductive resources, and as such, it is a zero-sum game. Males achieving more than the average mating success (i.e., mate numbers in excess of R) must do so at the expense of the mating success of other males (Wade 1995; Shuster and Wade 2002). The ESS model used to analyze the trade-off between immediate and delayed fitness gains (Maynard Smith 1977) fails in omitting the exchange of mates between male mating strategies. As a result of this failure, the ESS model requires that mean male fitness exceed that of females and thereby becomes internally inconsistent.

Wade (1979) suggested that males may be less parental than females because males increase their access to mates by decreasing their initial parental investment. That is, he postulated a trade-off for males between investment in precopulatory, reproductive competition and gamete size. Our revision of the classic ESS model for sex difference in parental care is consistent with this hypothesis as well as with the results of Parker et al. (1972), although this latter model for the evolution of anisogamy is usually presented as confirmation of parental investment theory. If the precopulatory hypothesis is true, differences in initial parental investment between the sexes represent a secondary rather than a primary cause for sex differences in mating and parental behavior. Differently put, differences in initial parental investment between the sexes are likely to arise from rather than lead to sexual selection favoring increased mate numbers in males and emphasis on parental care by females. This interpretation stands parental

investment theory on its head, an inversion justified by the results presented here. We believe it will have profound implications for future studies of sexual selection, parental care, and mating system evolution.

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