Sex and parenting: the effects of sexual conflict and parentage on parental strategies

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Adults of many organisms provide associated young with food and protection. Such care seems beneficial to the survival of young, and concluding that care is always favored under selection is easy. Nevertheless, in 1994 alone, over 150 scientific papers listed in *BioAbstracts* (weighted heavily toward birds) explored some aspect of parental care, belying the apparently simple proposition that this behavior is already well understood. Moreover, parental behavior is one of the most variable traits known: variation exists at all levels – among taxa, populations, the sexes and individuals. How can we understand this variation?

The extent of parental behavior is viewed as the outcome of potentially complicated trade-offs among fitness components (Box 1). The general theory that supports this view has stimulated considerable research in some key areas. For example, the hypotheses that care adversely affects survival of caregivers and increases offspring survival have received considerable support[3]. Trade-offs between care and mating, parent–offspring interactions, and parental manipulation of sex ratios are also the subjects of many recent studies[4]. There are exciting developments leading to new questions in each of these areas, but here we focus on two topics in which having two sexes is particularly provocative. First, because anisogamy (Box 2) is a conflict over parental care, parental care patterns in anisogamous species are affected by conflicts of interests between the sexes. Second, in some taxa (particularly in birds), patterns of matings lead to complicated patterns of relatedness between adults and associated young, thereby creating asymmetries in the benefits of care between males and females. We explore the ways in which recent theoretical and empirical work, employing new approaches or techniques, has stimulated exciting new ideas in these two areas.

Sexual conflict over parental care

In species with anisogamous sex, there will be conflict over care for offspring, which has effects on the selective forces acting on both sexes (Box 2). Models[7,8] that explore the consequences of such conflict on patterns of care produce several possible outcomes: either both parents care (because the costs and benefits are similar for both), neither parent cares, or one compensates at least partially for the reduced care of the other. Compensation has been demonstrated in many taxa[4], although it is usually not complete.

There is perhaps no more popularized aspect of animal behavior than the things parents do for offspring. Yet our understanding of the evolution of care is only rudimentary, perhaps because parental behavior is one of the most variable behavioral traits we know. Sexual reproduction, particularly in anisogamous species, has a major impact on variable patterns of care. Recent work on conflicts between the sexes over care and the consequences of variable paternity on paternal care has generated fascinating new ideas about the evolutionary forces acting on parenting.

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We are not aware of any studies showing directly that compensation has a cost, but experimental studies of the cost of reproduction have shown that increased parental expenditure results in reduced future reproduction[3]. Hence, compensation is probably a 'best-of-a-bad-job' solution, which means that conflict-induced selection could favor other, perhaps better, alternatives.

Several recent studies suggest some intriguing examples. One alternative to compensatory care is to reduce the benefits to the other parent of doing things other than providing care. For example, in house sparrows (*Passer domesticus*) some males manage to pair with two females[9]. For the female that settles later (secondary), this situation is costly because the male will provision at only one nest. Thus, secondary females are faced with having to provide sufficient care for the young by themselves. Primary females, however, mysteriously suffer heavy losses of clutches. The culprits are secondary females, who by committing infanticide cause redirection of the male's parental effort to their own offspring.

Another potential response to conflict over care is to manipulate the behavioral rules of thumb used by the other parent in providing care. In some birds, if offspring within a brood differ in age and weight, males tend to feed the older, heavier chicks, and females the younger and/or lighter. A recent study in blue tits (*Parus caeruleus*) found that experimentally induced hatching asynchrony increased female mortality between seasons[10], evidently because of the increased work females did in feeding younger, lighter offspring. Conversely, male survival was lower if broods hatched synchronously. Because there were no obviously older nestlings to be targeted by males, males helped with all the young, thereby increasing their overall contribution. Apparently, females decrease their costs and manipulate males into providing more care by delaying incubation until the last egg has been laid, which produces a smaller spread in hatching times. Additional research might clarify how males can dictate their preference for provisioning only the largest young when hatching is asynchronous, but apparently do not specialize on a subset of the offspring when they are similar in size, despite apparent benefits of doing so.

Sexual conflict over care could also favor mate choice (for a review see Ref. 11, pp. 203–206). Considerable attention has been focused on preferences for advertisements that serve as indicators of the ability to provide care. Recent

theoretical approaches to mate choice for indicator traits agree that such signals must be expensive in order to make them reliable, but the models' conclusions still differ in many respects (Box 3). This disagreement is mirrored by empirical studies revealing different relationships between a male trait and parental care (Box 4).

These conflicting results may arise from uncertainty about the underlying links leading to both the advertisement and parental care (Fig. 1). For example, female preferences might be influenced by good genes or good environments instead of or in addition to parental investment. Also, the amount of care a mate actually provides will depend not only on underlying quality (presumably reflected in the advertisement) but also on mating opportunities, which may be greater for mates with higher quality. Finally, environmental influences on the advertisement and on parental investment are important and potentially complicated, since some adornments are produced well before mating or parenting[12].

Choice for care need not always be indirect via some indicator trait. Such choice could be based on traits directly associated with care (for example, in many fish, females prefer to spawn with males that already have eggs, perhaps because those males will invest more if they have more eggs or are closer to beginning their brood cycle[2]). Individuals can even test the parental ability of prospective mates. In the Mediterranean blenny (*Aidablennius sphynx*), females lay a few eggs first and assess male parenting ability before spawning the balance of their clutch[21]. Such revision of mate choice following demonstration of male parenting was not found in an experimental test in a double-brooded bird[22], but more research is needed.

Parentage and parental care

Sexual conflict over care may arise because of differences in male and female mating behavior. A clear example of this occurs in many biparental birds, in which application of new molecular techniques has shown that patterns of matings often lead to variable paternity. Paternity in turn could affect patterns of male care, leading to new conflicts with females.

In the late 1970s, several models[7,23] suggested that paternity should have no effect on paternal behavior. For some time afterwards, interest in how parentage affects parental care languished. Recently, interest was renewed, by and large from the discovery of extensive extra-pair paternity in birds. Those early models are now receiving a second look, and it seems they were neither right nor wrong. Rather, the effect of reduced parentage appears to be conditional on both the abilities of prospective care-givers to assess parentage and the patterns of parentage over the life history of the individual (Box 5).

Box 2. Anisogamy, sexual conflict and parental care

Stable dimorphism of gamete sizes (**anisogamy**) arises because as soon as some individuals (females) begin investing energy into producing larger gametes with higher survival, selection begins to favor individuals (males) that invest in large numbers of small gametes instead[5,6]. This last step creates **sexual conflict** over investment in offspring survival – that is, a decrease in gamete size is favorable to males but reduces the fitness of females whose gametes fuse with small gametes. This is sexual conflict over investment in offspring quality via pre-zygotic care. Such conflict also occurs over post-zygotic care, because (1) with two potential care-givers, each benefits if the other provides more care, and (2) there often may be asymmetries in the costs of care to the two sexes, favoring reductions in care by one parent at the expense of the other. Because of the impact of changes in a trait in one sex on the fitness of individuals of the other sex, conflict over care is a force creating an opportunity for selection on trait(s) in the affected sex. The variety of traits that actually come under selection due to conflict remains a fruitful area for future research.

Box 1. Parental investment: trade-offs among fitness components

Evolutionary ecologists assume that natural selection favors behaviors that maximize the total expectation of lifetime reproductive success, assuming a stationary population. Parental care is an investment in present offspring, which may be traded off against investment in future components of fitness. Assuming a stationary population, age-specific reproductive value may be written as:

$$v_x = m_x + \sum_{t=x+1}^{\infty} \frac{l_t}{l_x} m_t \qquad (1)$$

where v_x is the total expectation of lifetime reproductive success of an animal of age x, l_x is survival from birth to age x, m_x is expected fecundity at age x, t is the index of age classes, and l_t/l_x gives the survival between ages x and t (Ref. 1). Eqn 1 can be re-written as:

$$v_x = m_x + \frac{l_{x+1}}{l_x} v_{x+1} \qquad (2)$$

where the ratio l_{x+1}/l_x represents survival from age x to $x+1$ (Ref. 2). v_{x+1} is the total expectation of reproduction from age $x+1$ to the end of the animal's life, which is devalued by the probability of survival from age x to $x+1$. Thus, eqn 2 states that total expectation of lifetime reproductive success of an animal of age x can be expressed in terms of two episodes in time: age x and age $x+1$. There are two points to be made from eqn 2. First, ecological trade-offs or constraints may prevent an animal from being able to optimize present and future reproduction simultaneously, which could create a trade-off between these fitness components and affect optimal strategies of parental care. Second, eqn 2 can be modified to model the day-to-day decisions of parental care. Time may be indexed over shorter intervals than age classes, such as days that offspring are under parental care. Thus, eqn 2 can simultaneously model trade-offs among breeding seasons, among breeding cycles within the present breeding season, and among offspring of different ages within the present breeding cycle.

The conditional nature of parentage and parental care seems to be borne out by those empirical studies in which parentage (paternity) has been assessed directly by DNA techniques. Contrasts between two subsets of these studies are particularly revealing. First, in the most thorough study of paternity and paternal behavior to date, Davies[26] and colleagues demonstrated that male dunnocks (*Prunella modularis*) in polyandrous trios will provide care in relation to their paternity. By removing males during parts of the female's fertilizable period, these researchers discovered that the male uses the extent of his mating access with the female as a cue to paternity. If he has mated with the female during the period between laying of the first egg and the last, then he usually will have sired some of the offspring and so will provide care. However, mistakes occur because each egg is fertilized the day before it is laid, making the actual start of the female's fertilizable period shifted from when eggs appear in the nest.

Second, Jamieson *et al.*[27] examined paternity and paternal care patterns in the similarly polyandrous pukeko (*Porphyrio porphyrio*) and found a somewhat different pattern. Males do not provide care in relation to paternity; each male in a trio copulates with the female, and although dominants obtained more copulations and sired more of the offspring, they did not mate-guard. Betas therefore obtained copulations and fertilizations in nearly all trios (in contrast to the dunnocks), but even though they tended to sire fewer offspring than alphas, they provided care as often as alphas.

Although superficially different, both dunnocks and pukeko appear to respond to paternity similarly; in dunnocks some beta males have little access to the female and sire no offspring – so providing care in those circumstances is not beneficial. In pukeko, all males usually copulate with the

female and sire some young, and so providing care may be beneficial as long as at least one young is a descendant. In dunnocks, the percent of mating access is a good predictor of paternity and thus is correlated with chick-feeding effort. Pukeko appear different; one possible reason is that mating access is a poorer predictor of paternity in pukeko than in dunnocks because greater variation in the intervals between the laying of successive eggs leads to greater uncertainty about when a female is fertilizable.

Contrasts between another set of studies are also revealing. Extra-pair fertilizations account for 55% of the young in reed buntings (*Embiriza shoeniclus*), a sometimes socially polygynous species with extensive biparental care[28]. Among broods matched by male (thereby eliminating the possibility that the results arise from the presence of low-quality males who might normally provide less care and also have lower paternity), provisioning was lower in broods with lower paternity. Similarly, male red-winged blackbirds (*Agelaius phoeniceus*) provide variable amounts of parental care and sire only 75% of the nestlings on their territories. In an Ontario population, males were less aggressive to potential nest predators at nests with extra-pair young than nests without (matched within males)[29]. The reduction in defense helps explain the fact that nests with extra-pair young failed significantly more often than nests with only within-pair young. In contrast to both studies, Westneat[30] found that male red-winged blackbirds did not vary their provisioning of food to offspring with respect to paternity, despite analyses that controlled for other variables known to affect paternal care.

We do not know yet why these studies differ, but one reason may be that the populations differ in the cues about paternity available to males. Males in New York may have very poor indicators of paternity. Perhaps male reed buntings and Ontario redwings have more information about their mate's copulation behavior. Alternatively, the difference between the two blackbird studies could arise because

the benefit curve for nest defense has a different shape than the curve for nestling provisioning (Box 5).

Most of the studies described above reported non-experimental associations between paternity and paternal behavior. Such investigations are initially important in revealing interesting patterns, but explanations for those patterns will probably require careful experimentation. Several workers have attempted to manipulate paternity itself or the information received by a male about his paternity. Detaining males during their female's fertilizable period is a popular experiment (reviewed by Ref. 31). The results have been mixed, with some studies showing an effect on paternal behavior[26,32], but others finding no effect[30,33]. Whittingham et al.[33] attempted to simulate cues to paternity by housing male tree swallows (*Tachycineta bicolor*) in cages near their nests where they could see their mate interact with other males. No effect on paternal behavior was found, perhaps because paternity has a threshold effect on optimal paternal effort (Box 5) or because the manipulation still did not adequately simulate natural EPC behavior. In a clever twist on removal studies that may have simulated a more natural cue, Wright and Cotton[31] caught female European starlings and held them briefly (20 min) in cages near a neighboring male. Controls were similarly manipulated before the fertilizable period. Unfortunately, the results are not clear; experimental males did not provision nestlings significantly less often than controls did, but there was a strong trend in that direction, and a significant difference between the sexes (experimental females appeared to increase their provisioning slightly).

The above studies examined patterns of paternity and paternal care among broods. To date, only three studies have tested the proposition that care might be directed preferentially to descendants within broods[26,28,34]. Westneat et al.[34] explicitly tested several ways in which such biases could occur, by video-taping male red-winged blackbirds bringing food to nestlings of known paternity. They found no evidence of either direct discrimination (see Box 5), or of any consistent pattern of provisioning via another variable (e.g. age or gender of the nestling) that might be correlated with paternity. Additional studies with larger samples could test these possibilities more thoroughly and with more confidence, but as yet there is no evidence that within-brood patterns of parentage influence parental care.
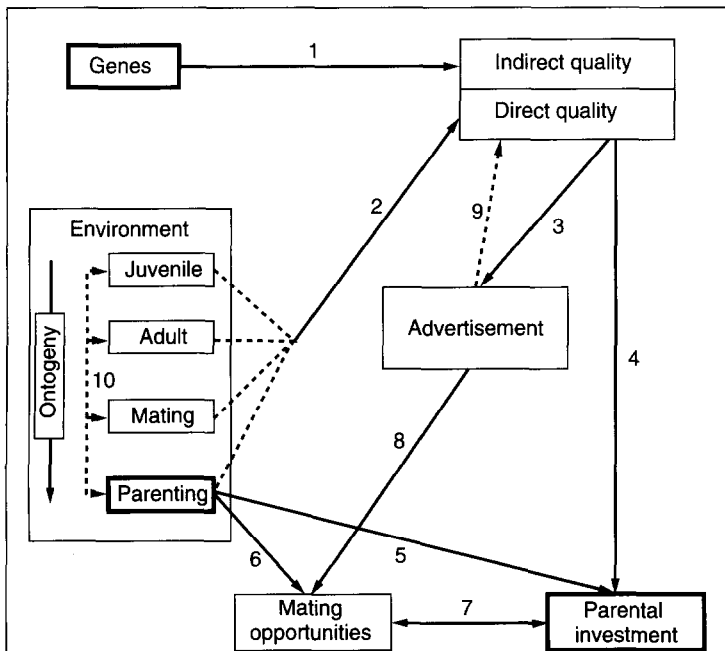
Fig. 1. Path diagram illustrating key links in a general model of mate preferences for advertisements. The advertisement is assumed to be expensive and hence is based on quality (with direct or indirect components). The advertisement is the object of female choice; females potentially benefit from preferring adorned males via factors outlined in bold (i.e. good genes, good environment during parenting, or good parental care). Mate choice for good parenting depends on the advertisement at the time of mating reliably indicating future parental investment (i.e. paths 3 and 4 reflect strong positive correlations). This will not be the case if: (a) quality and hence the advertisement are heavily influenced by environment (paths 2 and 3), but environmental influences on parenting are independent (e.g. path 5 is strongly positive but path 10 – the correlation between the aspect of environment important for the advertisement and that for parenting – is weak); (b) the adornment increases mating opportunities (path 8 is positive), which trade off with parental investment (path 7 is negative); and/or (c), the advertisement is sufficiently expensive that it uses up the resources available for parenting (joint effect of paths 3 and 9).

Box 5. Why is the effect of parentage on parental care conditional?

Both theory and empirical work indicate that parentage has variable effects on parental behavior. If an adult is not related to some of the juveniles that it might parent, then the benefit of parental behavior is clearly reduced. Why then is the effect of parentage variable? The answer is because models yield different results depending on assumptions about patterns of paternity and the types of responses available to prospective care-givers. Early models[7,23] assumed that (1) parents have no information about their relatedness to dependent juveniles, and (2) relatedness is invariant from one mating to the next. Relaxing these assumptions, however, has a major impact on the relationship between parentage and parental care[24].

If assumption (2) is relaxed, then even if parents do not assess parentage, relatedness still may have an effect through **non-facultative responses**, in which the level of care is set through evolutionary time[24]. This occurs if consistent patterns of parentage (e.g. over different ages) select for patterns of parenting (e.g. by age) that correlate with parentage. Such patterns are possible between and within broods. If assumption (1) is relaxed, then **facultative responses** are possible, via either *direct discrimination* in which a parent can directly recognize genetic descendants and provide care preferentially, or *indirect cues*, through which a prospective parent has general information about the likelihood of being the genetic parent. In either case, care might be reduced if prospects for alternatives are not similarly bleak.

Whittingham *et al.*[25] present results of a model that adds additional complexity to this picture. The function relating reductions in parentage to changes in optimal parental effort depends on the shape of the curve relating parental effort to the benefits of care. For a concave down benefit curve, progressive reduction in parentage in the present brood reduces the marginal value of parenting, causing a continuous decrease in optimal effort. For an S-shaped benefit curve, as parentage decreases there is a point at which there are two local optima with the same net fitness. This creates a discontinuity, and hence a threshold effect of parentage on parental effort.

Summary: the next generation of studies?

'Frustrating but fascinating' is an apt description of the picture that emerges from the current work on both conflict over care and the effect of parentage. It is frustrating to have different results from theoretical and empirical work both on mate choice for care and on paternity and paternal care. But this situation is stimulating, as there are many interesting hypotheses now ready to be tested, and we expect even more to arise as taxa other than birds receive more attention. For example, biparental species in a wider array of taxa should be scrutinized for behaviors other than compensation that are associated with conflicts over care. Studies of advertisements should investigate the underlying environmental influences on both the trait and parental investment and the effects of adornments on trade-offs with care. An interesting recent suggestion is that paternal care itself could be an advertisement[35]. In addition, in some insects, fish and birds, intra-specific brood parasitism occurs and reduces maternity. An investigation of maternal care in such cases would provide an instructive contrast with the studies of paternity and paternal care. Finally, if one parent does withhold parental care in response to a cue indicating reduced parentage, then sexual conflict over care might favor behaviors by the partner that make information on paternity less reliable. Thus, when male or female care is not allocated in relation to parentage, their mate's behavior may provide an important clue to why not.

One of the exciting aspects of the present state of behavioral ecology is that so many of the important questions now require an integrative perspective and a multidisciplinary array of research tools. Studies of both conflict over parental care and responses to reduced parentage provide superb examples of the benefits of approaching questions with a broad perspective and a willingness to use different techniques to solve problems. The combinations of modelling sexual conflict and patterns of relatedness, empirical studies of behavior, and, in the case of parentage, application of molecular genetic tools, have been especially fruitful. However, it is clear that the two topics we have reviewed here are likely to benefit more from an even broader conceptual view and additional tools being used in other areas.

Studies of parental strategies will also benefit from explicit consideration of the proximate mechanisms of behavior. The physiological bases and ontogeny of advertisements and the means by which parents can assess maternity or paternity are two prime examples. In addition, although evolutionary models have explicitly addressed some hypotheses, often they are drawn from a single, but limiting, perspective. For example, evolutionary stable strategy (ESS) models of games between the sexes make major assumptions about the types of traits involved. Application of quantitative selection models to such games might be a profitable prelude to uncovering other traits influenced by conflicts. Quantitative genetics has infrequently been applied to parental care because variation in offspring survival confounds heritable (genetic) and parental (environmental) effects. Recent expansion of theory that gets around these problems provides a powerful heuristic and statistical approach to analyses of parenting behavior[36] and might be helpful in exploring relationships as in Fig. 1.

These challenges are forcing new researchers to become broader and more sophisticated in their outlook. It is indeed a daunting and heady time for parental-care enthusiasts.

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Erratum

The most recent issue of *TREE* was, of course, published in January 1996, not January 1995
(as erroneously stated on the cover and p. 38). We apologize to all our readers for this
egregious error.