

Sexual Conflict between Parents: Offspring Desertion and Asymmetrical Parental Care

Tamás Székely

Department of Biology & Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom

Correspondence: T.Szekely@bath.ac.uk

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Parental care is an immensely variable social behavior, and sexual conflict offers a powerful paradigm to understand this diversity. Conflict over care (usually considered as a type of postzygotic sexual conflict) is common, because the evolutionary interests of male and female parents are rarely identical. I investigate how sexual conflict over care may facilitate the emergence and maintenance of diverse parenting strategies and argue that researchers should combine two fundamental concepts in social behavior to understand care patterns: cooperation and conflict. Behavioral evidence of conflict over care is well established, studies have estimated specific fitness implications of conflict for males or females, and experiments have investigated specific components of conflict. However, studies are long overdue to reveal the full implications of conflict for both males and females. Manipulating (or harming) the opposite sex seems less common in postzygotic conflicts than in prezygotic conflicts because by manipulating, coercing, or harming the opposite sex, the reproductive interest of the actor is also reduced. Parental care is a complex trait, although few studies have yet considered the implications of multidimensionality for parental conflict. Future research in parental conflict will benefit from understanding the behavioral interactions between male and female parents (e.g., negotiation, learning, and coercion), the genetic and neurogenomic bases of parental behavior, and the influence of social environment on parental strategies. Empirical studies are needed to put sexual conflict in a population context and reveal feedback between mate choice, pair bonds and parenting strategies, and their demographic consequences for the population such as mortalities and sex ratios. Taken together, sexual conflict offers a fascinating avenue for understanding the causes and consequences of parenting behavior, sex roles, and breeding system evolution.

Sexual conflict over care is a type of evolutionary conflict that emerges from the different interests of males and females in regard to parental care (Trivers 1972; Clutton-Brock 1991; Chapman et al. 2003; Arnqvist and Rowe 2005). The conflict arises when the young benefit from the effort of either parent, but each parent pays only the cost of its own effort, so that each par-

ent would have higher fitness if the other parent provides more care (Houston et al. 2005; Lessells 2006; Klug et al. 2012). Conflict refers to the way selection acts on the two sexes that have different optimum values in parental provisioning; between the two optima, sexually antagonistic selection operates (Lessells 2012). Sexual conflict over care can be seen as tug-of-war, be-

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cause each parent is tempted to pull out of care leaving the other parent to provide more care for the young (Székely et al. 1996; Arnqvist and Rowe 2005; Lessells 2012).

Sexual conflict over care seems to be the rule rather than the exception. The conflict may be resolved by one or both parents failing to adopt the optimal parenting for their mate and nonetheless remaining in conflict, or by both parents adopting the optima that suit their mate (i.e., exhibit the maximum provisioning possible). Examples of the latter conflict resolution (whereby the conflict is completely wiped out) are exceedingly rare and seem to be limited to three scenarios. First, conflict over care is not expected in obligate monogamy by both males and females so that the lifetime reproductive successes of both parents are identical. This may occur in semelparous organisms (i.e., both the male and the female put their resources into a single breeding event) or in iteroparous organisms with lifelong exclusive monogamy. Second, males and females might be genetically identical, so even though one or both sexes are polygamous, polygamy would benefit the same genome whether it is in the male or the female phenotype. Third, parental care is cost-free and thus parents provide maximum level of care (P Smiseth, pers. comm.). However, few, if any, organisms fit these restrictive assumptions, and thus conflict-free parenting seems exceedingly rare in nature: (1) some level of polygamy (by males, females, or both sexes) appears to be widespread; (2) the reproduction by genetically identical individuals (clones) as separate sexes (males and females) seems unlikely although not impossible if sex is determined environmentally; and (3) care provisioning, as far as we are aware, does have costs that discourage parents from providing their absolute maxima for a given batch of offspring.

Parents may have conflicting interest over caring or deserting the young, the amount of care provided for each young, the number of simultaneous mates, the size and sex ratio of their brood, and the synchronization of birth for a clutch or litter of young (Westneat and Sargent 1996; Houston et al. 2005; Klug et al. 2012; Lessells 2012). Conflict between parents

over care is usually labeled as a postzygotic conflict although resources had been already allocated into the gametes before fertilization as part of parental provisioning (Clutton-Brock 1991); other examples of postzygotic conflicts include infanticide and genomic imprinting (Chapman et al. 2003; Tregenza et al. 2006; Lessells 2012; see Palombit 2014).

Studies of conflict over care are fascinating for at least four major reasons. First, parental care is diverse. There is great variation both between and within species in the types of care provided, duration of care, and the sex of the care-providing parent (Wilson 1975; Clutton-Brock 1991; McGraw et al. 2010; Royle et al. 2012), and sexual conflict is thought to be one of the main drivers of this diversity. Second, parental care is one of the core themes in breeding systems and sex role evolution, and it is increasingly evident that parental care can only be understood by dissecting the entangled relationships between ecological and life-history settings, and the variety of mating and parenting behavior (Székely et al. 2000; Webb et al. 2002; Wedell et al. 2006; Jennions and Kokko 2010; Klug et al. 2012). Third, parental care was (and is) one of the test beds of evolutionary game theory. Numerous models have been developed to understand how parents interact with each other and with their offspring (Trivers 1972; Maynard Smith 1977; Houston and Davies 1985; Balshine-Earn and Earn 1998; McNamara et al. 1999, 2000; Webb et al. 1999; Johnstone and Hinde 2006; Johnstone et al. 2014). Parental care research is one field in which empiricists are extensively testing the predictions of evolutionary game theoretic models in both the laboratory and wild populations (Székely et al. 1996; Balshine-Earn and Earn 1998; Harrison et al. 2009; Klug et al. 2012; Lessells 2012; van Dijk et al. 2012), although the congruence between theoretical and empirical work is not as tight as often assumed (Houston et al. 2013). Finally, parental care—wherever it occurs—is often a major component of fitness, because whether the offspring are cared for or abandoned has a large impact on their survival, maturation, and reproduction (Smiseth et al. 2012). Therefore, parental care (or the lack of it) may



have an impact on population productivity and population growth and influences the resilience of populations to various threats (Bessa-Gomes et al. 2004; Veran and Beissinger 2009; Blumstein 2010). Thus, understanding the behavioral interactions between parents and the fitness implications of these interactions is highly relevant for population dynamics and biodiversity conservation (Alonzo and Sheldon 2010; Blumstein 2010).

Sexual conflict over care has been reviewed recently (van Dijk and Székely 2008; Lessells 2012; Houston et al. 2013). Here, I focus on three issues that have not been extensively covered by previous reviews: (1) why sexual conflict over care occurs in some environments, whereas in others parental cooperation appears to dominate; (2) how can one detect sexual conflict over care; and (3) what are the implications of sexual conflict over care for macroevolution. I view causes and implications of parental care primarily from empirical perspectives; there are excellent reviews on the rich theoretical literature (Lessells 2006, 2012; Klug et al. 2012; Houston et al. 2013). My intention is not to be comprehensive; instead, I use selected examples to illustrate salient features of conflict over care. I focus on ecological and evolutionary aspects; for a discussion of the genetic and neuroendocrine bases of parental care, see Adkins-Regan (2005), McGraw et al. (2010), and Champagne and Curley (2012). I prefer to use the term “parental care” instead of “parental investment,” because the latter, as admitted by Trivers (1985), is extremely difficult to estimate empirically and thus may have a limited use in empirical studies (Mock and Parker 1997; McGraw et al. 2010). The term “parental investment” can be deceptive, if used without directly demonstrating the full costs of care. The term “parental care” is less restrictive, because it refers to any form of parental behavior that appears to increase the fitness of an offspring and is likely to have evolved for this function (Clutton-Brock 1991; Smiseth et al. 2012). In this review, I focus on families in the narrow sense (i.e., two parents and their offspring), although in numerous organisms the families are more extensive and may include several generations of

offspring living together and/or unrelated individuals that assist the parents rearing the young.

SEXUAL CONFLICT AND PARENTAL BEHAVIOR

Conflict between parents may occur in species with identical sex roles or with different sex roles driven by the different cost and benefits of care for males and females arising from the sex differences in physiology, ecology, and life history (Fairbairn et al. 2007; King et al. 2013). Conflict may occur in organisms that have no parental care, assuming that at least some parental care (by the male, the female, or both parents) would improve offspring survival and thus parental fitness. Conflict may also occur in organisms in which only the male, the female, or both parents provide care. I start this section by emphasizing the diversity parental care strategies and then explore how conflict over care could influence the emergence and maintenance of this diversity.

Diversity of Care Strategies

Parental care is one of the most diverse social behaviors (Wilson 1975; Reynolds et al. 2002; McGraw et al. 2010; Smiseth et al. 2012). The type of care, the duration of care, and the involvement of one or both parents in various care activities are all highly variable both within and between animal taxa. Conflicts between parents and the resolution of these conflicts offer powerful approaches to understand this diversity (Trivers 1972; Maynard Smith 1977; Arnqvist and Rowe 2005; Lessells 2012). Whereas the majority of invertebrates and many vertebrates do not provide any care for the fertilized embryo beyond supplying the eggs with nutrients, the species that do exhibit care have amazing adaptations. There are excellent recent reviews on parental care in both vertebrates and invertebrates (Balshine 2012; Trumbo 2012), and, thus, here I focus on selected examples that illustrate some of this variation and comment on their relevance to the study of sexual conflict.

Studies have discovered an immense variety of care strategies, and discoveries of novel forms

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and types of parental care are still being made (Fig. 1). For instance, tropical frogs have some of the most diverse reproductive and parental care systems among animals (Wells 2007), and parental care is thought to have evolved independently at least 41 times (Balshine 2012). Some species of frogs prepare a foam nest for their eggs, whereas others attend the eggs laid on leaves that overhang streams or are viviparous and give birth to small froglets. Parents in other frog species brood the eggs on their back, in their vocal sac, or in their stomach, transport the tadpoles and froglets, or urinate on the eggs to prevent them from desiccating (Summers et al. 2006). Parental care can be a major occupation for male and female frogs for substantial periods of time when they regularly check the development of tadpoles, and the female may lay trophic eggs to nourish the tadpoles (Brown

et al. 2010). Parents may also seek out pools that are free from competitor larvae and cannibalistic tadpoles and move their own tadpoles to predator-free pools if necessary (Summers et al. 2006; Brown et al. 2010).

Because the reproduction of a vast number of species has not been studied in detail, especially those that live in difficult-to-access habitats such as tropical forest canopies, the deep sea, or caves or soil, new forms of parental care are waiting to be discovered. For example, in caecilians, a little-studied subterranean amphibian group, it was not known until recently that mothers incubate their eggs in underground burrows and that the altricial hatchlings feed for an extended period of time on the modified and lipid-rich outer layer of the skin of their mother using specialized dentition (Kupfer et al. 2006; Wilkinson et al. 2013).

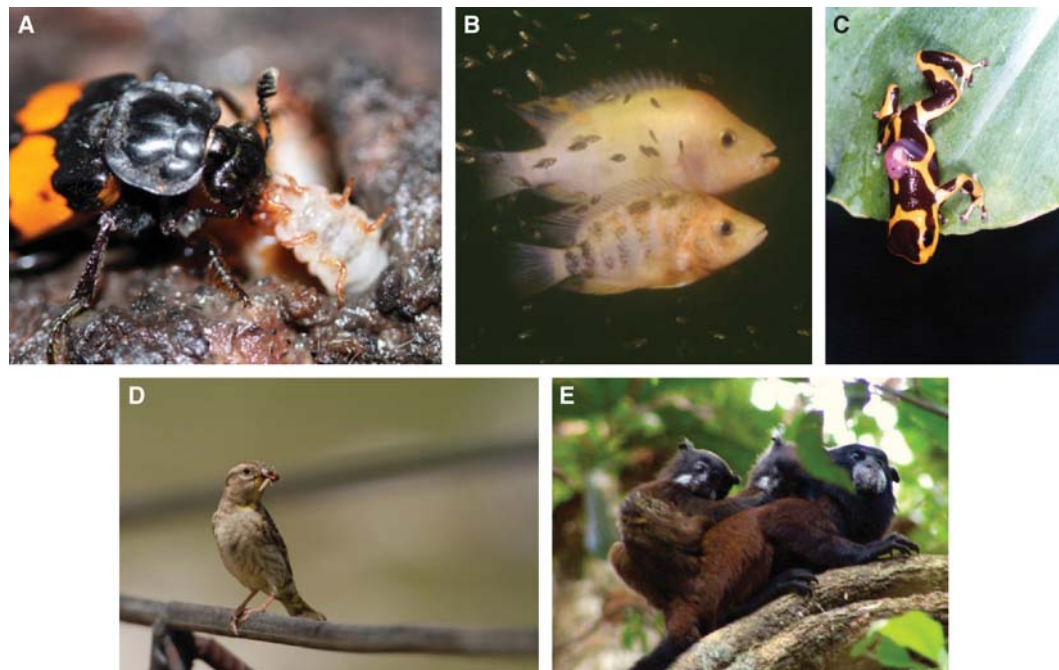


Figure 1. Diverse forms of parental care. (A) Begging behavior in *Nicrophorus vespilloides* burying beetle. (B) Midas cichlid (*Amphilophus citrinellus*) couple looking after the young. (C) Male Peruvian mimic frog (*Ranitomeya imitator*) carrying a tadpole to a pool on his back. (D) Female rock sparrow (*Petronia petronia*) feeding her nestlings. (E) Saddle-backed tamarin (*Saguinus fuscicollis*) carrying twins. (From Per Smiseth, A; Ad Konings, B; Rainer Schulte, C; Adriano De Faveri, D; and Mojca Sojan-Dolar, E.)



Care can be provided for a long time not only in whales, elephants, and primates, including humans, in which it may last up to several decades (de Waal and Tyack 2003; Mitani et al. 2012), but also in invertebrates. Mother whip spiders *Phyrnus marginemaculatus* protect their young for at least 11 months (Trumbo 2012). During such an extended period, the parent–infant relationship that is initially driven by offspring demand and the parents' readiness to provide care may shift toward an alliance between the parent(s) and the siblings. For instance, in scorpions, groups of young can help the mother to subdue large prey (Trumbo 2012).

It is usually assumed that evolutionary transitions in duration of care or type of care are driven by sex-specific costs and benefits, and, thus, the transitions are the result of changes in ecology and life history of males, females, or both sexes. However, it is plausible that some of these transitions are largely (or entirely) the result of changes in male and/or female behavior as they are trying to resolve the conflict. First, for a given set of costs and benefits, multiple patterns of care may occur in a population; this may be the result of mixed evolutionarily stable strategies (ESSs) (Webb et al. 1999), to different behavioral interactions between parents (McNamara et al. 1999; Johnstone et al. 2014), or to social interactions between parents and other members of a population that can stabilize different ESSs in a coevolutionary process that involves mate choice, mating behavior, and parental care (McNamara et al. 2000; van Dijk et al. 2012). Second, an important insight from evolutionary game theory is that as males (or females) attempt to attain their respective fitness optima, they may change the cost and benefit functions for their mates, and thus influence the fitness landscape for the opposite sex (McNamara and Weissing 2010). Although it is not known whether the first and/or the second processes are more likely generating multiple care patterns in wild populations, it does seem that conflict resolution at both ecological and evolutionary timescales are influencing the transitions between different parenting behaviors.

Why (Not) Care?

Sexually antagonistic selection is one of the theories that behavioral ecologists use to understand the emergence and maintenance of diverse care patterns (Trivers 1972; Maynard Smith 1977; Houston et al. 2005; Lessells 2012). As each sex is moving toward its parental care optima given the behavior of its mate and the rest of population, it elicits a response from the other parent and vice versa. Selection may operate on these changes. Actions and responses that lead to higher reproductive success are likely retained in the population. However, similarly to other types of sexual conflict, it is difficult to infer conflict from behavioral patterns alone, because the parental behavior exhibited by the sexes does not tell anything about the difference between the optima of males and females (Lessells 2012). Therefore, observations that one parent deserts and all care is provided by the other parent or that both parents share care equally do not tell too much about the extent of conflict. Furthermore, because sexual conflict refers to selection process, conflict may not have behavioral signs; for instance, aggression between parents may (or may not) indicate the intensity of conflict over care.

The direct evidence for sexual conflict over care is scarce, because few studies have estimated the fitness outcomes of parenting behavior from the perspectives of both the male and the female (see the section Detecting Conflict over Care). The hedonistic breeding systems of Eurasian penduline tits (*Remiz pendulinus*) may illustrate fitness consequences of various parenting options (Fig. 2). In this small passerine bird (body mass of ~9 g), either the male or the female abandons the clutch and renests with a new mate shortly after desertion. Remating is common; both males and females may have up to five different mates in a single breeding season (Persson and Öhrström 1989). A puzzling aspect of penduline tit breeding biology is the large number of deserted clutches. About 30%–40% of clutches are abandoned by both parents and these clutches produce no young. High frequencies of biparental desertion have been observed in all studied populations to date, so most

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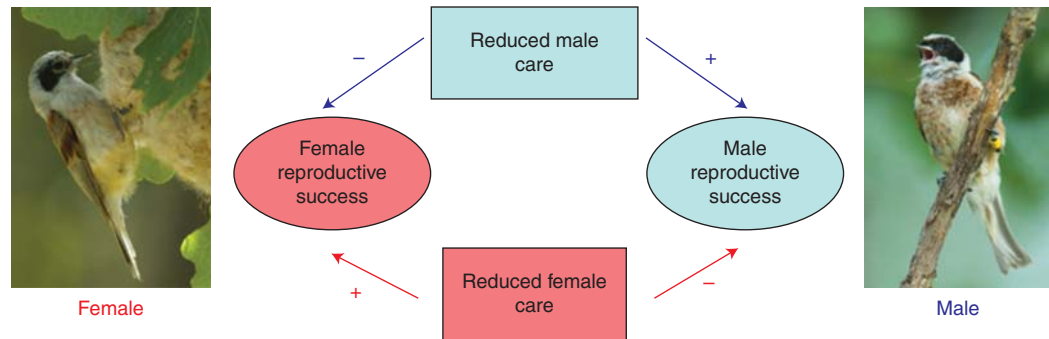


Figure 2. Fitness consequences of various parenting options. The impact of reduced care (i.e., offspring desertion) on reproductive success of Eurasian penduline tits (based on Szentirmai et al. 2007). Positive and negative signs indicate improvement and reduction, respectively, on reproductive success of males (blue) and females (pink). (From René van Dijk.)



likely it is part of natural breeding behavior (van Dijk et al. 2010a). Whereas in many animal populations predation of eggs or young is the major sources of breeding failure, in penduline tits, biparental desertion is a substantially more common cause of breeding failure than predation of eggs or young, or any other cause of nest failure.

Szentirmai et al. (2007) estimated the reproductive success separately for caring and deserting penduline tits using data from an intensely studied population in Hungary. Deserting the clutch increased the reproductive success of the deserting males, because many of these males found a new mate and renested. Desertion, however, was costly to deserted females, because they either deserted the clutch themselves and thus doomed the offspring to death, or stayed with the offspring for about one month and cared for them until they became independent (Szentirmai et al. 2007; van Dijk et al. 2012). The fitness consequences of desertion and caring in males are mirrored by fitness consequences in females. Deserting the clutch increases a female's own reproductive success but reduces her mate's reproductive success. Therefore, there is a temptation for both male and female penduline tits to abandon the mate and seek a new partner, although en route to increase their own reproductive success by deserting and subsequently remating, they risk the survival of their existing brood. The high frequency of

biparentally deserted clutches suggests that the parents' gamble often did not work out. Extra-pair paternity does occur in penduline tits (van Dijk et al. 2010b), although the frequency of extra-pair young (EPY) is comparable between male-cared and male-deserted young, suggesting that EPY does not bias the estimated reproductive success of deserted versus cared nests.

Species with variable care patterns, like penduline tits, offer great opportunities to quantify fitness implications of care and desertion and to assess the extent of sexual conflict. Similarly, the highly variable care patterns (both within and between species) in assassin bugs, cichlid fishes, poison dart frogs, and shorebirds may emerge via conflict over care whereby a shift in costs and benefits of care for one sex (or for both sexes) can flip from one pattern of care to another. Although different costs and benefits of care for male and female, and thus difference in sex roles, are not essential for sexual conflict over care, these taxa offer biological systems in which the fitness implications can be evaluated. Because selection is expected to produce male behavior that is the best response to female parental behavior, the changes in cost and/or benefits of care in one sex are likely to induce change in parental behavior of the other sex, somehow analogous to the sexually antagonistic prezygotic selection (see Gavrilets 2014; Sirot et al. 2014).



Theoretical models suggest that social behavior itself can generate shifts. There are situations in which both uniparental care and biparental care are ESSs, and they can coexist in a population (McNamara et al. 2000; Kokko and Jennions 2008; Klug et al. 2012; van Dijk et al. 2012). The presence of several care patterns in a single population is consistent with theoretical results (see the section Diversity of Care Strategies), although alternative explanations of coexisting caring strategies are also possible—for instance, age-dependent care strategies and/or temporal or spatial variation in costs and benefits of care for different members of the population.

Parental care, however, is a complex trait even though theoretical models and comparative studies often reduce care to a single (or a few) variable(s). Representing care as a single trait is problematic, because parents may provide different types of care and these different components may evolve independently from each other (Smiseth et al. 2012; Székely et al. 2013). Parents may also divide the tasks so that each parent specializes on particular tasks; male dung beetles, for instance, excavate the ground under the dung ball, whereas the female covers the ball with soil (Trumbo 2012). Such specialization can reduce conflict between males and females and maintain biparental care (Lessells 2012; Barta et al. 2014).

Manipulation and Parental Tactics

Males and females may use a variety of tactics to entice (or coerce) their mate to increase their care. In biparental species, a female may attempt to monopolize the parental care of its mate (Chapman et al. 2003; Arnqvist and Rowe 2005). Females may solicit superfluous copulations from their mates (Eens and Pinxten 1996) or interfere with their mate to prevent them from attracting new females (Slagsvold and Lifjeld 1994). To impose monogamy on her mate, female burying beetles *Nicrophorus defodiens* bite and attempt to push the male off his signaling perch and interfere with his attempt to release pheromones attracting additional mates (Arnqvist and Rowe 2005). Similarly, females

may be hostile toward other females so as to keep their mate's care provisioning for their own offspring (Sandell and Smith 1996; Liker and Székely 1997). Males, however, can counteract female strategies by intervening directly and keeping peace between females (Walter and Trillmich 1994), or by attracting a new female away from their current family so that their existing female cannot interfere with the new female.

Parents may manipulate their mates' behavior to extract more care using two strategies. First, paternally imprinted genes in placental mammals may facilitate embryonic growth so that the developing embryos extract more resources from the mother than would be optimal for her (genomic imprinting; see Haig et al. 2014). An analogous manipulation has been proposed for birds. Females are hypothesized to deposit elevated levels of androgens in the eggs to increase chick begging behavior, so that the chicks extract more care from the male (Schwabl 1996; Groothuis et al. 2005). The latter hypothesis has been tested by several studies, and, currently, little evidence supports it (Lessells 2006; Laaksonen et al. 2011). Instead of improving offspring viability, elevated androgen level appears to reduce offspring viability in the long term (Ruuskanen et al. 2012).

Second, parents may strategically handicap themselves to extract more care from their mate (Barta et al. 2002). By reducing their own body condition, females can put their mate in a difficult situation. If the male abandons, then the female alone cannot rear the young so the brood would die ("credible threat"; Barta et al. 2002). Although body condition has been shown to relate to parental care (e.g., males in low body condition reduce their care [Steinegger and Taborsky 2007]), the existence of strategic handicapping by lowering body condition has not been shown.

Although the larger (or physically stronger) individuals in a pair can "force" the smaller parent to care, reports of physical coercion are rare (Awata and Kohda 2004). There may be three reasons for this. First, harmful behavior, coercion, and manipulation are expected to be weaker in conflict over care than in conflict over

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mating (Lessells 2006), because, in the former, a harmful behavior to a mate would reduce not only the mate's reproductive success, but also the actor's reproductive success. Second, the manipulated parent could retaliate and harm (or eat) the offspring and thus defeat the objective of the manipulation in the first place. Third, enforcing a complex behavior such as care that may be tuned to a specific offspring age and demand seems exceedingly difficult. In contrast to other forms of coercion that seem straightforward (e.g., keeping another animal away from a resource [e.g., food or water] or forcing another individual to copulate) and specific behaviors that appear to have evolved to achieve these objectives (e.g., aggression), forcing an animal to carry out a complex and fine-tuned behavior such as parental care seems less likely.

DETECTING SEXUAL CONFLICT OVER CARE

Because sexual conflict may involve adaptation and counteradaptation, it is thought that these processes and their results will be difficult to observe (Chapman et al. 2003; Arnqvist and Rowe 2005). Theoretically, the extent of conflict can be estimated in two ways: (1) by quantifying the parental optima for males and females and then estimating the difference between the two optima (the conflict “battleground”; Godfray 1995); or (2) by estimating the fitness reduction in males, females, or both sexes caused by conflict (“conflict load”; Lessells 2006). Ideally, both battleground and conflict load should be estimated simultaneously to reveal both the behavioral differences caused by conflict and their fitness implications; however, no study appears to have performed both. Much of our current knowledge is based on either of these estimates or on indirect inferences of the conflict.

Observations

Fitness implications of different duration, type, or intensity of care can be established by studying wild or laboratory populations. Studies have compared the reproductive success of different care patterns (e.g., male-cared vs. female-cared, uniparental vs. biparental families, no care vs.

care; Clutton-Brock 1991; Eldegard and Sonerud 2009; Pogány et al. 2012), assuming that a difference between the two estimates indicates the lost reproductive success because of the unwillingness of one or both parents to provide care.

Offspring desertion by the male, female, or both parents is a common behavioral strategy that occurs in wide range of taxa (insects, fish, frogs, birds, and mammals) (Clutton-Brock 1991; Székely et al. 1996; Korpimäki et al. 2011), and studies suggest that conflict over care is involved (Houston et al. 2005; Griggio et al. 2008; King et al. 2013). The social environment may modulate the benefit of desertion. High density of potential mates is expected to favor desertion, whereas low density may temper desertion (Owens 2002). Social environment, however, may offer biased mating opportunities given that adult sex ratio (ASR) is skewed in numerous organisms (Donald 2007; Székely et al. 2014), and the biased ASR favors desertion by one sex over the other. For instance, male-biased ASR was thought to explain female-biased desertion in birds (Box 1) (Pilastro et al. 2001; Kosztolányi et al. 2011; Liker et al. 2013; Parra et al. 2014). Furthermore, the benefit of desertion may differ between the sexes, if one sex needs more time to recover from breeding than the other (Gubernick et al. 1993; Balshine-Earn and Earn 1998).

In principle, comparing the two strands of benefits (care vs. desertion) that lie at the core of parental care evolution (Clutton-Brock 1991; Székely et al. 1996) should indicate the fitness consequences for males and females, and thus tell to what extent these fitness peaks differ between males and females (the “battleground”). The timing of desertion and the sex of the deserting parent are highly variable between species and populations (see the section Diversity of Care Strategies) (McGraw et al. 2010; Balshine 2012; Trumbo 2012), and these variations provide excellent opportunities to assess the benefits of care versus desertion. However, there are caveats. Although the examples in the next paragraph are framed in the context of discrete parental decisions (i.e., care vs. desertion; Székely et al. 1996), similar arguments can be made for other aspects of care such as duration of care and type of care.



BOX 1. CONFLICT AND COOPERATION BETWEEN KENTISH PLOVER PARENTS

The Kentish plover, *Charadrius alexandrinus*, is a small shorebird (body mass of 40–44 g) that exhibits a variable mating system and parental care (Lessells 1984; Székely and Lessells 1993; Amat et al. 1999). Two to three eggs are laid in a small scrape on the ground. Both parents incubate the eggs, although, after hatching, one of the parents usually abandons the brood and renests with a new mate. Thus, in a single population, three types of brood care (biparental, male-only, and female-only) and three types of mating system (social monogamy, sequential polygamy by the male, and sequential polygamy by the female) are observed. DNA fingerprinting shows that extra-pair paternity is rare (<4% of chicks) (Küpper et al. 2004); and, thus, the social mating system reflects genetic mating system. A series of experiments and observational studies have been performed in the natural habitat to clarify the roles of environmental and life-history variables that may influence the extent of conflict and parental cooperation (Table 1).

Kentish plovers live in temperate and subtropical habitats, and their breeding habitat includes salt flats around Mediterranean lakes and deserts in which ground surface temperature may exceed 50°C (Amat and Masero 2004). Preventing the eggs from overheating is a major challenge, and Al-Rashidi et al. (2011) hypothesized that exposure to heat may select for biparental incubation. To test this hypothesis, they experimentally manipulated the exposure of eggs to sun by shading the nest with a small bush (Fig. 3). The results were consistent with the hypothesis, because the extent of biparental incubation was reduced in the shaded nests.

To compare the benefits of deserting for male and female plovers, unmated plovers were experimentally created, and the time they took to find a new mate was observed (Székely et al. 1999). Unmated females remated after a substantially shorter time than unmated males, suggesting that mating opportunities are significantly better for female than male plovers. This experimental result is consistent with a demographic study that estimated a heavily male-biased adult sex ratio (Kosztolányi et al. 2011).

A recent experimental study in closely related plover species found different mating opportunities. In white-fronted plover *Charadrius marginatus* males and females mating opportunities were not different, whereas in Kittlitz's plover *Charadrius pecuarius*, the remating time was longer in females than in males (Parra et al. 2014). The latter results suggest that mating opportunities—and thus the benefits from deserting—can be substantially different in closely related species.

Table 1. Different components of parental care in the Kentish plover

	Uniparental care	Biparental care	Type of evidence	Reference
Life history				
Family size	Small	Large	Experiment	Székely and Cuthill 2000
Timing of breeding	Early	Late	Observation	Székely and Cuthill 2000
Ambient environment				
Environmental harshness	Mild	Harsh	Experiment	Al-Rashidi et al. 2011
Food abundance	Poor	Rich	Observation	Kosztolányi et al. 2006
Predation rate	Low	High	Observation	Amat et al. 1999
Social environment				
Adult sex ratio	Strongly biased	Less biased	Observation	Kosztolányi et al. 2011

Both parents cooperate in incubating the eggs, although after hatching, most broods are cared for by a single parent (either the male or the female). Desertion is beneficial only for the deserting parent and costly to its mate.

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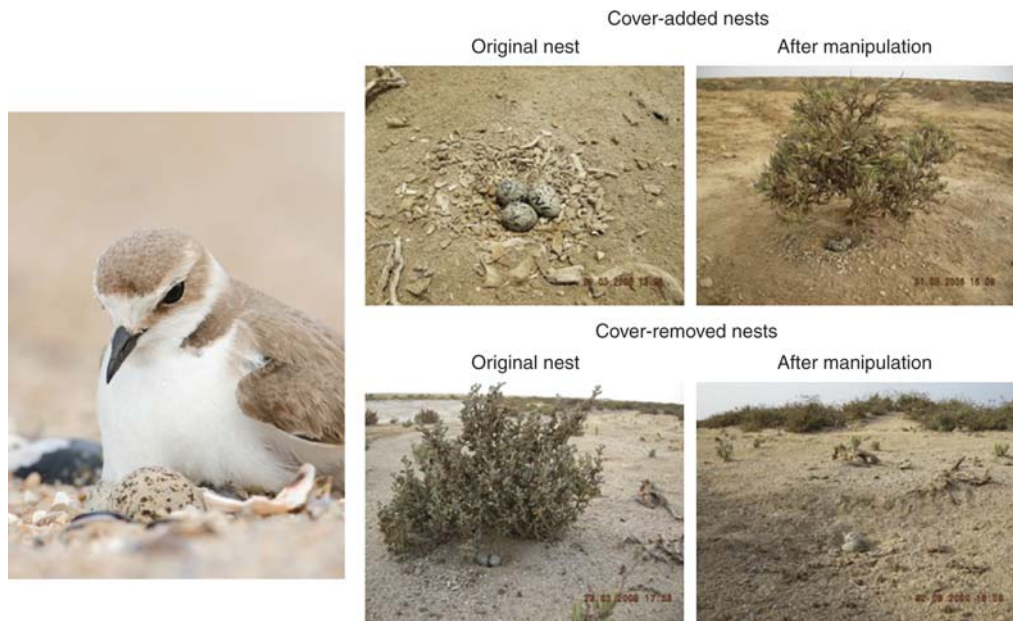


Figure 3. Female Kentish plover incubating the eggs (*left*) and experimental manipulation of nest cover (*right*). (*Left*, from Hugo Amador; *right*, from Al-Rashidi et al. 2011; reprinted, with permission, from Elsevier © 2011.)

First, comparing the fitness consequences of caring and deserting for a selected group of animals may not represent the population as a whole. Thus, the best fathers may decide to care, whereas the most attractive fathers may decide to desert and find another mate. Similarly, a single parent may be able to provision the young on a territory with abundant food, whereas both parents may be needed to feed the young on a poor territory (Eldegard and Sonerud 2009). Second, the benefit for a given parent, let us say the male, from deserting depends on his mate's response. Will she continue rearing the offspring or desert herself? Therefore, estimating the fitness consequences of caring and deserting should be performed at various response levels of the other parent. This is rarely feasible, because wild populations rarely exhibit all behavioral strategies. Third, the benefits of caring and deserting may manifest over a long time period, whereas studies usually estimate short-term fitness consequences (van Dijk et al. 2012). One may need to investigate several generations to reveal the full scale of

costs and benefits. This can be challenging especially in long-lived animals or in polygamous species, in which the number of mates may proliferate into an extensive network of breeders for which reproductive success estimates are required.

How males and females play out these conflicts is rarely studied in detail. Unlike divorce in humans that can be an extended and convoluted process, desertion in nonhuman animals can be rapid (van Dijk et al. 2012). Studies are needed to work out on a behavioral scale how parents interact, whether they may escalate or converge in response to each other's behavior (Johnstone et al. 2014).

Experiments

To overcome the limitations of observational studies, two kinds of manipulations were used to perturb parental behavior and seek the consequences of perturbation on parental behavior and reproductive success. First, experimenters manipulated the benefits of matings—for in-

stance, making males (or females) more attractive to the opposite sex (Smith 1995; Griggio et al. 2010). For example, by setting up an additional nest box close to a pair of common starlings (*Sturnus vulgaris*), male starlings reduced their involvement in care and sang to attract a new mate (Smith 1995).

Second, researchers manipulated parental attendance (e.g., by removing or handicapping one parent) to investigate the consequent changes in partner's behavior and fitness (Harrison et al. 2009). By experimentally removing one parent, Royle et al. (2002) created uniparental and biparental broods in zebra finches *Taeniopygia guttata*. They showed that male chicks reared by a single parent were more attractive as adults to females than males reared by two parents, suggesting that the conflict between male and female parents results in lower-quality offspring.

Males (or females) were handicapped (or removed) in various biparental organisms (insects: Rauter and Moore 2004; Smiseth et al. 2005; Suzuki and Nagano 2009; fish: Mrowka 1982; Itzkowitz et al. 2001; birds: Sanz et al. 2000; Harrison et al. 2009; mammals: Wynne-Edwards and Lisk 1989; Gubernick and Teferi 2000). These experiments produced two main insights. First, although there is large variation between species in response to manipulation of parents, mates of handicapped parents tend to compensate; however, the compensation is usually not complete (Harrison et al. 2009; but see Mrowka 1982). This is consistent with theoretical arguments; partial compensation is necessary to maintain biparental care (Houston and Davies 1985; McNamara et al. 2002; Lessells 2012). Second, although parental care tends to be asymmetric in that females usually take a larger share than males (Queller 1997), across the species compensatory responses of males and females are not different (Harrison et al. 2009). This is in contrast with three species of *Nicrophorus* beetles, in which the males but not females compensated for the lost care of their mate (Lessells 2012). Presumably, in the latter species, the females are already working close to their maximum capacity while they are still attended by their mate, and once their mate is

removed they cannot improve their workload (Lessells 2012).

In burying beetles, male desertion may be actually beneficial for the female, because staying males eat some of the carcass that would be available for the larvae (Boncoraglio and Kilner 2012). Therefore, females may have coevolved to anticipate desertion by their partner so that they now benefit from the male's absence. However, in wild populations in which males and females roam freely, the male presence at the carcass may be beneficial by helping to protect both the carcass and the developing larvae from intruding males that may kill the offspring (Trumbo 2007).

Although experimental studies have intrinsic advantages over observational studies, these experimental studies also suffer from drawbacks. First, manipulations of a focal sex (let us say, males) should be designed to reveal the fitness implications at various levels of response (here, by the female). Existing experiments, however, usually manipulate one sex and estimate fitness implications at the self-selected level care of its mate. Because parents cannot be forced to care, manipulating systematically the care of both parents simultaneously seems to be exceedingly difficult. Second, complex mating patterns (such as the one exhibited by Eurasian penduline tits) exacerbate this difficulty, because full exploration of parental behavior and their fitness implications would mean experimental manipulation not only in one family, but in all subsequent families of the focal individuals. Therefore, the best empirical system for experimental evaluation of battleground and conflict load would be short-lived, predominantly monogamous animals that only breed a few times throughout their life.

Comparative Analyses

Phylogenetic comparative analyses have been used to detect the tug-of-war between males and females (Arnqvist and Rowe 2005). In shorebirds, which exhibit unusually diverse parental care strategies ranging from male-only care to biparental and female-only care, the duration of male care is traded off against the

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duration of female care (Reynolds and Székely 1997), so that evolutionary decreases in male care are associated with increases in female care and vice versa. Although the duration of care is not necessarily a good indicator of parental effort, this pattern is consistent with theoretical predictions that each parent should reduce its involvement in care, whereas its mate is selected to compensate the lost care. An implication of the phylogenetic trade-off between male and female care is that males and females do adjust their care to the care of their mate, consistent with experimental manipulations in contemporary populations (Harrison et al. 2009; Kosztolányi et al. 2009; Trumbo 2012).

Whether the tug-of-war over care occurs may depend on phylogenetic plasticity. Webb et al. (2010) showed that care strategies are more variable in species with short rather than long offspring development. Furthermore, taxa with high variation in care duration exhibit variable care patterns, because male involvement in care is associated with an extensive period of parental care (Webb et al. 2010).

Artificial selection and experimental evolution are powerful approaches to investigate both the causes and the implications of prezygotic sexual conflict (Holland and Rice 1999; Chapman et al. 2003; Arnqvist and Rowe 2005; Rowe and Day 2005), although there might be confounding effects because of different sources of conflict (e.g., interlocus or intralocus conflict). Despite their widespread use in studies of prezygotic conflict, they have not been used to investigate conflict over care. There may be two reasons for this gap. First, fast-breeding laboratory species often do not exhibit care (e.g., many flies, beetles, and nematode worms), or if they do have some care (e.g., mice *Mus musculus*), there is little flexibility in males' and females' involvement that would capture the parental care variation seen in numerous populations in nature. Second, although care-related behaviors have been artificially selected in poultry (e.g., Champagne and Curley 2012), such work usually targets only females, so it is not straightforward to extrapolate from these single-sex selection experiments to fitness implications for both sexes.

THE IMPLICATIONS OF SEXUAL CONFLICT OVER CARE FOR MACROEVOLUTION

Sexual conflict over care, similarly to other types of sexual conflict, is expected to facilitate diversification, speciation, and rapid evolution (see Gavrillets 2014). Although a specific theory has not been developed to investigate macroevolutionary consequences of conflict over care, the sexually antagonistic selection—the adaptations and counteradaptations to increase male or female fitness—is thought to influence care strategies, somehow analogous to prezygotic sexual conflict (Chapman et al. 2003). For instance, the diverse reproductive modes in frogs and fish are related to parental care (Goodwin et al. 1998; Gomez-Mestre et al. 2012), and conflict between parents is a candidate driver of this diversity (see the section Diversity of Care Strategies). However, a caveat is that it is extremely difficult to nail down whether speciation (or diversification) is largely (or exclusively) a result of conflict over care, because phylogenetic studies are correlational and they do not identify causation. The most convincing approach would seem to be experimental evolution, although as I noted above, this approach has not been used in studies of conflict over care.

Conversely, offspring desertion and uniparental care may reduce productivity of the population (Holman and Kokko 2013). As an extreme example, the 30%–40% clutch loss in Eurasian penduline tits because of conflict (Szentirmai et al. 2007) is likely to impact on population productivity and increase the risk of population decline and/or extinction. Furthermore, reduced productivity because of the reluctance of males to provide care appears to be costly across wide range of bird species, because female-only care leads to a 20% reduction of productivity compared with other types of care (Sibly et al. 2012).

ECOLOGY OF CONFLICT AND COOPERATION

Although theory tells us that family life is rife with conflicts, the intricate pair-bonding ceremonies and the tender (often affectionate) relationships between males and females observed



in some insects, fish, birds, and mammals leave no doubt that males and females coordinate their behavior; they do cooperate not only to copulate and make temporary liaisons but also to rear their young for extended time periods and to prepare them for the adult life. Studies of cooperation have a venerable history (Hamilton 1964; Wilson 1975; West et al. 2007; Székely et al. 2010), and one may view parental behavior as a balance between factors that facilitate conflict and those that facilitate cooperation (see below). The various costs and benefits of care can be translated into that of the former or the latter. There are excellent reviews on the costs and benefits of care (Clutton-Brock 1991; Wedell et al. 2006; Reichard and Boesch 2007; Royle et al. 2012); thus, here I focus on one issue: how ambient environment and social environment may interactively shape cooperation and conflict between parents.

On the one hand, parents tend to cooperate in rearing the young in a harsh physical environment (i.e., extreme cold or heat, very humid or dry) (Wilson 1975; Clutton-Brock 1991). In such environments, the fitness consequences of not cooperating fully are severe, so there will be little conflict. However, convincing evidence for this hypothesis is scarce, because manipulating the physical environment can be challenging. One of the few experimental studies manipulated the exposure of parents and their eggs in a desert environment by shading some nests or removing the shade from other nests (Al-Rashidi et al. 2011). The results were consistent with the harsh environment hypothesis. At the experimentally exposed nests, parental cooperation increased, whereas at shaded nests, parental cooperation was reduced. The need of the young may also influence parental cooperation. When substantial parental resources are needed (e.g., food or protection), biparental care tends to evolve (Thomas et al. 2005; Brown et al. 2010).

Different skills of the parents may also facilitate parental cooperation (parental role specialization; Lessells 2012; Trumbo 2012). If one parent specializes in providing one type of care (e.g., feeding the young), whereas the other parent specializes in a different task (e.g., defending the offspring), this stabilizes biparental

care (Barta et al. 2014). Finally, long lifespan and durable pair bonds correlate with biparental care of the young (Ens et al. 1996; Port and Cant 2013), suggesting that in long-lived animals retaining the mate for future breeding is beneficial.

On the other hand, high mating opportunities and promiscuity tend to destabilize parental cooperation and reduce the incentive to provide care in one or both parents. Adult sex ratios are often unbalanced, and in female-biased populations like in many mammals, males are at an advantage in finding a new mate (Donald 2007; Kokko and Jennions 2008; Székely et al. 2014). When one sex has higher mating opportunity than the other, the favored sex tends to capitalize from the opportunity to leave the other parent to look after the young (Balshine-Earn and Earn 1998; Pilastro et al. 2001; Kosztolányi et al. 2011; Liker et al. 2013). In addition, promiscuity tends to temper the males' willingness to provide care (Queller 1997; Kokko and Jennions 2008), although caring for somebody else's offspring may still be the best option if finding a new mate is difficult or if the male can somehow selectively assist his own offspring (Møller and Cuervo 2000; Kamel and Grosberg 2012).

The breeding system of a ground-nesting small shorebird, the Kentish plover, illustrates how conflicts and cooperation may interactively influence parental care (Box 1). In the Kentish plover (as in most shorebirds), both parents incubate the eggs, and biparental care of the eggs for a substantial part of incubation seems essential for any young to hatch. Because hatchlings are precocial and capable of feeding themselves, the demand for care is reduced so that one parent (the male or the female) may desert the family after hatching. Brood desertion benefits only the deserting parent, because the deserting parent typically remates and renests with a new mate, whereas the deserted parent stays with the chicks until the chicks die or fledge at ~4 wk of age. Desertion is costly for both parents because brood survival is lower after desertion than before desertion (Székely and Williams 1995). On top of this cost of desertion, there are additional costs for the deserted parent because it can be killed by predators while it de-

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fends its young, and he/she loses mating opportunities.

The fitness implications of Kentish plover parental care may illustrate two important points (Box 1). First, the costs and benefits of care are often complex and they may change over the course of breeding season. In addition, costs and benefits may differ between populations because of different ambient environments and social environments. To reveal these costs and benefits, one may need to combine observations with experiments to expose the full magnitude of fitness implications for both males and females. As I argued above, fitness implications alone do not determine the outcome of parental conflict, so that the behavioral interactions between male and female parents need to be investigated as well. Second, the conflict and cooperation between parents are played out in a breeding population in which breeding and nonbreeding individuals interact, and thus it is important to understand how parenting decisions relate to mate choice, competition for mates, and pair bonding. Thus, conflict over care needs to be approached as influencing (and being influenced by) other aspects of breeding behavior (McNamara et al. 2000; Houston et al. 2005; Alonzo and Sheldon 2010; Jennions and Kokko 2010; Székely et al. 2014).

FUTURE DIRECTIONS

Although immense progress has been made recently in studies of conflict over care, certain areas are ripe for major advances. First, care is a complex and multidimensional social behavior, and analyzing the implications of the different components is likely to give novel insights into conflicts over care and conflict resolution in regard to both parental strategies (battle-ground) and fitness (conflict load). Theoretical, experimental, and phylogenetic analyses of this multidimensionality are long overdue.

Second, parental conflict is played out in a population, and it is essential to reveal the interactions between a focal pair (or family) and the rest of the population (Székely et al. 2000; Alonzo 2010; Jennions and Kokko 2010). Because behavioral actions have demographic con-

sequences (e.g., maturation, reproduction, and mortalities), rolling up the complex relationships between sexual selection, cost of care, sex-specific mortalities, and breeding system dynamics seems especially important (Liker et al. 2013). The causes of parenting behavior and their consequences at the population level are likely to be complex, although detailed studies of populations that are monitored for a long time now offer the opportunities to tease apart these feedback relationships (Klug et al. 2012; Liker et al. 2013).

Third, although studies established some of the genetic, hormonal, and neuroendocrine causes of parental care, much remains to be discovered about the mechanisms of care and parental interactions.

1. New advances in genomics and neuroscience are offering unparalleled insights into the genetic, genomic, and neural causes of parental behavior (McGraw et al. 2010; O'Connell and Hoffman 2012), and using these approaches, one may work out how each sex is attempting to maximize its own reproductive success and/or how they influence (or manipulate) their mate's behavior.
2. Learning of parenting and sex roles should receive more attention—for instance, when, how, and why young animals learn to be a parent. Learning and genetic mechanisms of care are probably interwoven in a complex way (Székely et al. 2010), and revealing these interdependencies will establish the pathways of how males and females may respond to each other's behavior.
3. Male and female parents may monitor each other's behavior, and alter their own strategy in response to the other parent. Such repeated interactions (“negotiation”) (McNamara et al. 1999; Lessells 2012) have received much theoretical attention, although how these interactions play out in nature is not known in detail (but see Johnstone et al. 2014).
4. Parents may manipulate their mate's behavior or take on self-imposed handicaps. Experimental studies are needed to test these theoretical scenarios.

Fourth, whereas various studies provide behavioral evidence of conflict over care, few studies have quantified the magnitude of conflict in terms of reproductive outcomes for both males and females.

1. Studies are needed that contrast the theoretically expected versus observed behavior and reproductive success of males and females. Also, detailed studies are needed to work out the assumptions and fitness implications such as the costs and benefits of care. For instance, a common assumption of theoretical models is that the benefit of care follows a saturating curve, whereas the cost function is accelerating (Houston and Davies 1985; Lessells 2012). Although these assumptions seem perfectly plausible, I am not aware of any empirical study that has estimated the shape of these functions over a range of realistic parameter values. This may be important because theoretical predictions may depend on the shape of the cost and benefit functions. Using behavioral norms seems to be one of the promising approaches to quantify these functions (Westneat et al. 2011).
2. Artificial selection and experimental evolution are powerful approaches, although no study seems to use these approaches for sexual conflict over care. Using appropriate model organisms, selection experiments can reveal immense information about the genetic and behavioral structures and fitness implications that underlie conflict over care and conflict resolution.
3. Furthermore, theoretical, comparative, and experimental studies are needed to work out the potential implications of sexual conflict over care for speciation and extinction, somehow analogous to comparable works in prezygotic conflict.

Finally, parental care has only been investigated in detail in <1% of animal species that populate the planet, and our knowledge is biased toward taxa that are readily studied (McGraw et al. 2010; Balshine 2012; Trumbo 2012). The parental care of organisms living in extreme en-

vironments (e.g., deep sea, extreme heat, or freezing temperatures) deserve further attention. Information from a wider range of organisms coupled with recent advances in phylogenies and phylogenetic comparative analyses are likely to reveal novel aspects of conflict over care.

CONCLUDING REMARKS

Conflict over care is central to the understanding of sex roles and breeding systems. Research in this field is rapidly advancing because of the tractability of many biological systems to experimental manipulations, long-term field studies, and phylogenetic comparative analyses. Parental care is also one of the well-known behaviors used as real-life examples in evolutionary game theory, and empiricists are making laudable efforts to match theoretical predictions with experimental results.

Research on parental care and on its implications is making a fundamental contribution to evolutionary biology as exemplified by the study of Trivers (1972) on parental investment that ignited a paradigm shift and became one of the most cited studies produced in this broad field. Parental care research will continue to benefit from new theoretical advances, methods and techniques, and is likely to remain a prosperous field in evolutionary biology.

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