

Sexual conflict over parental care: the role of negotiation between parents in determining their relative share of care



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Abstract

Since both parents are related to their shared offspring but are unrelated to each other, both benefit from their partner taking on most of the care for their shared offspring, resulting in sexual conflict over parental care. This conflict can lead to different patterns of care, with each parent having to decide whether to provide care, and if so, how much. There is a huge amount of variation in parental care provisioning. So can sexual conflict over parental care explain these different patterns of care? Two factors that have been assumed to play a role in this for a few decades already are discussed first – remating opportunities (1) and paternity (2) - after which I focus on a more recent development in this field, which is the study of interactions between parents on a behavioural time-scale (3). Including the behavioural interactions between parents is necessary to understand the decisions parents make within a single breeding event, as opposed to the pattern of care that develops over evolutionary time. Negotiation models have provided us with predictions of how a parent should respond to a change in parental effort by its partner. However, there is a lack of match between these predictions and empirical data, especially in the case of biparental care. Possible explanations for this are discussed, including models that have extended on negotiation models in an attempt to explain the variety of responses that are found.

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Introduction

The idea that the relation between the sexes is not necessarily one of cooperation, but can be one of intense conflict as well, has received considerable attention over the last decades (Chapman *et al.*, 2003). Sexual conflict arises because the sexes differ in their evolutionary interests. One situation in which males and females can have highly differing interests is when deciding if and how much care to provide for their offspring. Trivers (1972) was the first to suggest that the evolution of parental care is strongly influenced by sexual conflict. This sexual conflict over care becomes apparent in pairs that do not mate for life and where the male and female parent thus have differing reproductive interests. Care by the parent is a costly behaviour, both in terms of energy and in terms of lost opportunities for remating. Hence, although care increases the survival of the parent's current offspring, it leads to a decrease in its future reproductive success (Trivers, 1972; Clutton-Brock, 1991). Since both parents are related to their offspring, they both benefit from their young having a higher chance of survival and reproduction. On the other hand, the survival and (non-shared) future reproduction of their partner has no effect on their fitness, as they are not related. Therefore, the optimal situation for each parent would be for their partner to take on most of the parental care, causing sexual conflict between the parents (Wedell *et al.*, 2006).

There are several ways in which sexual conflict over parental care can be resolved. First of all, each parent has to make the decision whether to stay and care for the offspring, or to desert. If it chooses to stay, its offspring most likely will have a higher chance of survival. If it chooses to desert, the parent saves resources by not providing care, and might have the chance to remate, thereby increasing its reproductive success (Griggio, 2007). The possible outcomes of this decision are four different patterns of parental care: no care (i.e. both parents desert), uniparental care by the female (i.e. male deserts), uniparental care by the male (i.e. female deserts), and biparental care (Westneat & Sargent, 1996). For biparental care, there can also be variation

in the amount of care that is provided by each sex.

The patterns of care vary greatly between species, as well as within species, and even within single populations. For example, in a population of penduline tits, *Remiz pendulinus*, Persson & Öhrström (1989) reported both types of uniparental care, with 48% of the nests receiving female-only care and 18% receiving male-only care, while the remaining 34% of the nests were deserted by both parents. Szentirmai *et al.* (2007) found similar values of biparental desertion for a population of this species. However, the most common pattern of care in birds is biparental care; in over 90% of all bird species both parents provide care to the offspring together (Székely *et al.*, 2007). In other taxa however, biparental care is less common. For example, biparental care occurs in only 9% of all mammals, with maternal care being by far the most common pattern of care in mammals (91%) (Reynolds *et al.*, 2002). Also in teleost (bony) fish, biparental care occurs in only 3% of the species, with the majority of species providing no care at all (79%) (Reynolds *et al.*, 2002). However, within teleost fish, there again is variation in the pattern of care, with biparental care occurring in 40% of cichlids for example (Reynolds *et al.*, 2002). Thus, patterns of parental care seem to be highly variable.

The question that follows from this huge variation in parental care provisioning, is whether sexual conflict over parental care can explain these different patterns of care? Previous studies on the topic of sexual conflict in relation to parental care have already suggested several factors that might play a role. These factors might influence the decision of parents to either desert or care (and subsequently, how much care to provide), and thereby they might determine the observed pattern of care. In this thesis, I give an overview of the most important factors that play a role in how sexual conflict can lead to different patterns of care, starting off with two factors that have already for several decades been generally assumed to play a role in this: remating opportunities (1) and the share of paternity (2). This thesis will however have its

main focus on short-term interactions between the parents (3). These behavioural interactions have only been included in theoretical models in the last decade or so, and therefore this is a more recent development in this field. Comparing the predictions from these models to the empirical results that have been found can show which findings still remain unexplained in this field of research, providing us with an excellent starting point for future research.

1. Remating opportunities

Trivers (1972) already recognized that the chance of remating during the breeding season could play an important role in a parent's decision to desert or stay. Trivers claimed that if the chances of remating are high, especially for the male parent, it may be beneficial to leave shortly after copulation, when the breeding attempt has cost him hardly anything yet, whereas the female has already invested a lot more by producing and laying eggs (Figure 1). However, this argument suffers from the Concorde fallacy, which states that past investment is irrelevant in the decisions parents make, and only future pay-offs matter in the decision making (Kokko & Jennions, 2008). But although Trivers' reasoning about initial investment was incorrect, he was right about the fact that parents can risk failure of the brood if there is a large enough chance to remate and start another brood.

Studies since Trivers' paper have yielded results in accordance with the hypothesis that greater remating opportunities result in higher levels of desertion. Szentirmai *et al.* (2007) showed that both male and female penduline tits often desert their brood, and for both sexes desertion increased their reproductive success while it decreased that of their deserted mate. For both sexes, sequential desertion resulted in them having more mates, and thus more offspring, at the end of the breeding season. Sexual conflict is so intense in the studied population that it often results in both parents leaving (roughly a third of the nests), but the potential benefit of additional mating seems to be so high for the deserting individuals that it is worth the risk of a brood failing.

Several studies have also included an additional factor that can play a role in the trade-off between the value of the current brood and remating opportunities; the time in the breeding season. For example, Pogány *et al.* (2008) found lower levels of desertion by male penduline tits late in the season compared to early in the season. In line with this, Székely and Cuthill (2000) found that further into the breeding season, Kentish plover (*Charadrius alexandrinus*) broods have a lower survival probability and remating opportunities for the female are also lower. Because of this change in the costs and benefits involved, the trade-off between the current brood and remating opportunities

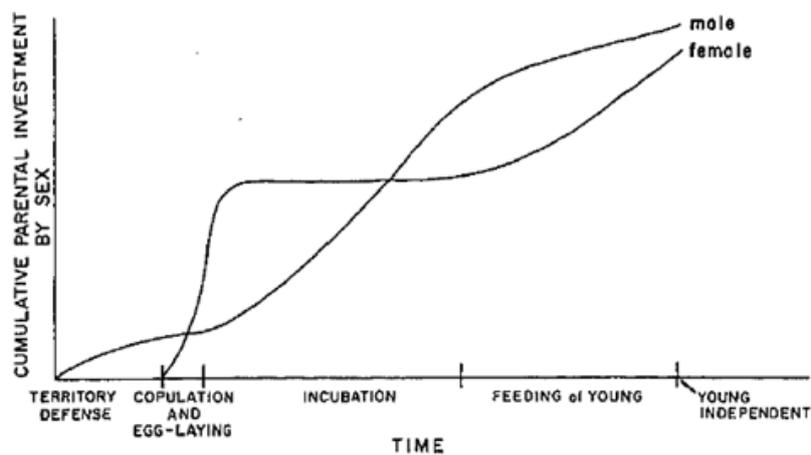


Figure 1 Cumulative parental investment for a male and female parent as a function of the different stages in a single breeding event. The parental investment shortly after copulation is much larger for the female parent, because of the high costs associated with egg-laying. (from Trivers, 1972)

plays a less important role in broods later in the season.

The studies that I have discussed so far involve complete brood desertion by one of the parents. However, additional mating opportunities do not necessarily lead to desertion, but can also cause a parent to decrease its share of parental care while still being present and providing some level of care for its current brood (Magrath & Komdeur, 2003). Numerous studies on the topic have provided us with evidence that there is indeed a trade-off between parental effort and additional mating effort (e.g., Magrath & Komdeur, 2003; Olson *et al.*, 2008). When the opportunity for additional matings is high, selection favours parents to allocate more time and energy to additional mating (either by attracting additional mates or by gaining extra-pair copulations), and therefore they reduce their share of parental care for their current brood (Magrath & Komdeur, 2003). Similarly, providing male zebra finches, *Taeniopygia guttata*, with access to extra-pair females resulted in courtship behaviour by these males, as well as copulation with these females in several cases. Providing males with extra-pair copulation opportunity was associated with a decrease in their contribution to incubation (Hill *et al.*, 2011).

Remating opportunities are an important factor in determining the pattern of care that is observed in a population. There is a strong link between remating opportunities and levels of care. However, several additional factors have also been proven to play a role in the amount of care that is provided by each parent. Therefore, I will discuss additional factors (level of paternity (2) and negotiation between parents (3)) that are also needed to fully understand the dynamics of patterns of parental care.

2. Level of paternity

The idea that the level of paternity is variable and that this can in turn lead to variable levels of paternal care has received a lot of attention over the last few decades as well (Westneat & Sargent, 1996). A review by Griffith *et al.* (2002) revealed that extra-pair paternity is extremely common in birds, with extra-pair

offspring being found in roughly 90% of all bird species. When paternity is variable, a male might be providing care to a brood that also contains offspring from other males, and thus his own share of paternity will be low for this brood. The benefit this male gains from the brood having higher survival is lower than when all the offspring would have been his. Therefore, it could be in the male's best interest to reduce its amount of care.

The development of DNA techniques has provided us with the ability to directly assess paternity (Westneat & Sargent, 1996). A famous example of where this technique has been put to use is in a study by Davies (1992), where the amount of care that male dunnocks (*Prunella modularis*) provided was directly related to their paternity, which they seemed to assess by the mating access to their female.

However, although studies such as that by Davies (1992) seem to have led to the general assumption that males decrease their amount of care when they have a lower share of paternity *and* when they can expect to have higher paternity in future broods, overall there is a lack of evidence for this (Alonzo, 2010; Alonzo & Heckman, 2010). Alonzo and Heckman reported the most extreme deviation from this initial hypothesis, with male ocellated wrasse, *Symphodus ocellatus*, increasing paternal care when sperm competition

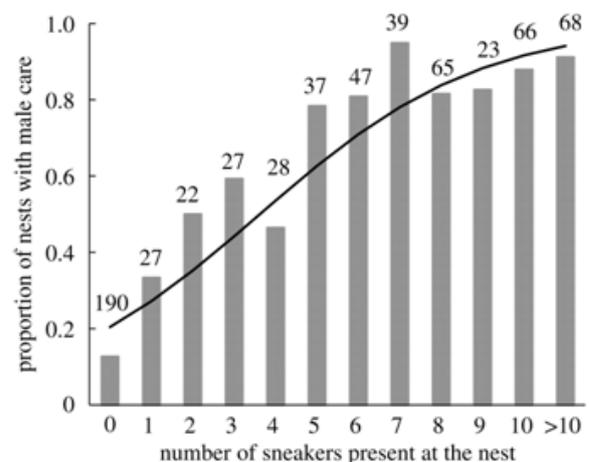


Figure 2 Male care increases with the presence of sneakers at the nest. Bars indicate the observed proportion of males caring for the nest, and the solid line the predicted relationship between number of sneakers and the probability of male care. Numbers above the bars are the sample sizes. (from Alonzo & Heckman, 2010)

(measured as the number of sneakers present) had been highest, and paternity was thus lowest (Figure 2). A literature survey by Alonzo (2010) revealed that less than half of the studies on the relation between paternity and paternal care did indeed find evidence that paternal care decreased with decreasing paternity, while the other half did not find such an effect.

A possible explanation for the lack of evidence for decreasing paternal care with decreasing paternity is that males may not always be able to accurately assess their share of paternity, because they either are not able to use direct paternity cues (e.g. kin recognition), or because the indirect paternity cues (e.g. presence of other males, or their mate's behaviour) are not reliable enough (Alonzo, 2010). Therefore, paternity is only a weak predictor of parental care, and paternity alone cannot explain the variable patterns of care.

3. Behavioural interactions between parents: negotiation

There have not only been empirical, but also many theoretical studies on the topic of sexual conflict over parental care. These theoretical studies have provided us with models that attempt to predict how sexual conflict can lead to different patterns of parental care. One of the first models was that by Houston & Davies (1985). This model assumes that there is a single bout of investment, and so both parents are able to make the decision of how much to care for their offspring only once, and they are not able to adjust their decision to the investment made by their partner (Lessells & McNamara, 2012; Houston & Davies, 1985). In this model, the investment of each parent is fixed in ecological time, and therefore this type of model is referred to as a "sealed bid" model.

Later models (McNamara *et al.*, 1999, 2003) do allow parents to respond to each other's investment on a behavioural time-scale throughout the breeding attempt. In such models, the parents engage in a series of interactions in which they negotiate the final level of care, and therefore these models are referred to as negotiation models. These

models do not focus on the evolutionarily stable *actions* of the parents (i.e. the actual amount of parental care provided after negotiation), but on the evolutionarily stable *negotiation rules* (McNamara *et al.*, 1999).

Before negotiation models were introduced, numerous empirical studies did in fact already focus on the interactions that take place between parents within a single breeding season. For example, they studied the response of a parent to a decrease in care by its partner (e.g., see Harrison *et al.*, 2009). However, most of these studies incorrectly assumed that they were testing the predictions made by Houston and Davies' model (1985), failing to realise that this model predicted the pattern of care that evolves over *evolutionary* time, as opposed to the decisions parents make in their relative share of care over *ecological* time. The latter is what many of these studies actually focused on.

Nonetheless, these studies, and also empirical studies since then, have provided us with proof that parents do indeed negotiate over their share of parental care. McNamara *et al.* (2002) briefly reviewed the empirical evidence on negotiation at that time and concluded that there was evidence that parental decisions are not made independently. Since then, there have been considerably more empirical studies on the topic. In one such study, male penduline tits were experimentally removed from their nests and the behaviour of their deserted partner was studied (Czyz, 2011). The decision of the female parent to desert or stay was determined by the male's decision to desert (or in this case, its experimental removal), indicating that female penduline tits respond to their partner's investment on a behavioural time-scale. House sparrow (*Passer domesticus*) pairs also negotiate over the duration of bouts of incubation, during visits from the parent that is currently on recess to the parent that is incubating (Schwagmeyer *et al.*, 2008). Kosztolányi *et al.* (2009) also report Kentish plover parents adjusting their level of incubation after the experimental increase of the level of incubation by its mate, which is consistent with negotiation models. Houston *et al.* (2005) refer to several additional studies that report partial compensation by a parent

after its partner had been experimentally handicapped. These results serve as proof that the decisions parents make about parental care are made through a negotiating process.

In their review, Houston *et al.* (2005) stress the importance of including behavioural interactions between the parents, especially in theoretical studies. To my knowledge, no review on the topic of behavioural interactions has been published since that review. Studies have made a lot of progress since then however, and I will focus on both empirical and theoretical studies in the rest of this thesis. An important subquestion in this field of research is the extent to which a parent will increase or decrease its amount of care in response to a change in effort by its mate. In the next sections, I will try to answer the question of how behavioural interactions between the parents determine whether both parents provide care, and if so, how much each parent decides to care.

3.1 How *should* a parent respond to a change in care by its partner?

According to negotiation models, a change in the amount of care by one parent should affect the behaviour of the other parent as well (McNamara *et al.*, 1999). If one parent changes its level of care, there are four different possible ways in which the other parent can adjust its behaviour (Houston *et al.*, 2005; Harrison *et al.*, 2009; Johnstone & Hinde, 2006):

- It can compensate completely for its partner's change in care so that the total amount of care remains unchanged (full compensation).
- It can compensate partially for its partner's change in care, leading to a decrease in the total amount of care if the partner reduced its care, or an increase in the total amount of care if the partner increased its care (partial compensation).
- It can keep providing exactly the same amount of care as it did before, thus keeping its feeding behaviour unchanged (no compensation).
- It can match the change in behaviour of its partner (matching).

Desertion can be seen as an extreme reduction in the level of parental care, with the parent reducing its care by the maximum amount. In this case, the four possible responses of the deserted parent are the same as above, with matching meaning that the deserted parent also deserts the brood.

Theoretical prediction: biparental care

According to negotiation models, when following the evolutionarily stable response rules, a reduction in the amount of care that is provided by one parent (while biparental care is still maintained, i.e. no desertion) should result in partial compensation by the other parent (McNamara *et al.*, 1999; Akçay & Roughgarden, 2009). So if one parent decreases its amount of care, this should result in the other parent increasing its care, but by a smaller amount than what the other parent decreased it with.

This response makes sense if you consider what would happen if a parent would fully compensate for a decrease in its partner's effort. In that case, a reduction of parental care would not have negative fitness consequences for the parent that reduced care, since the young would still receive the same total amount of care. The parent that reduced its care would be better off than the other parent, thus "exploiting" the other parent. This cannot be an evolutionary stable strategy (ESS) and therefore partial compensation is the response that is predicted by negotiation models (Houston *et al.*, 2005; Lessells & McNamara, 2012). An interesting result of this partial compensation is that negotiation in biparental care thus reduces the overall amount of care provided for the offspring (McNamara *et al.*, 1999; Lessells & McNamara, 2012).

Theoretical prediction: desertion

So according to negotiation models, a parent should only partially compensate for a reduction in care by its partner to prevent being exploited. However, if one of the parents decides to desert the brood entirely, the other parent is expected to respond to this by increasing its parental care the best it can (Griggio & Pilastro, 2007; McNamara *et al.*, 2003). This means that a parent should provide

more care when its partner is gone than when its partner is present while not providing any care. An interesting prediction of these negotiation models is that young might in some cases even be better off with one parent than with two (McNamara *et al.*, 2003).

3.2 How does a parent respond to a change in care by its partner?

Numerous models have thus suggested how a parent *should* respond to a change in care by its partner, but how *does* a parent respond to this? Hereafter, I will provide an overview of the empirical studies that have investigated the response of a parent to a change in the amount of care by its partner.

Experimental methods

Two main types of experiments have been used to investigate the response of parents to reduced parental care by their partner: mate removal and handicapping (Harrison *et al.*, 2009). Mate removal has been used to study the response to being deserted by their mate, whereas handicapping has been used to study the effect of reduced care by the partner in the case of biparental care. Handicapping experiments can be carried out by for example clipping feathers or attaching extra weight (Kosztolányi *et al.*, 2009), thereby making parental care more demanding, or by diverting the male's attention away from parental care by for example using testosterone implants (Harrison *et al.*, 2009; Schwagmeyer *et al.*, 2008), or by manipulating extra-pair copulation opportunity (Hill *et al.*, 2011). Although in biparental broods studying the response to a change in the level of care by the partner is mostly accomplished by handicapping the partner (leading to a decrease in its share of care), a few studies have managed to *increase* the level of care by the partner, for example by cooling the nest while that partner was incubating (Kosztolányi *et al.*, 2009), or by using playback of extra begging calls whenever the partner visited the chicks (Hinde, 2006).

Houston *et al.* (2005) pointed out that there was a lack of experiments combining mate removal and handicapping. Combining these two methods could provide us with a better understanding of the way parents

negotiate over care. This is because according to theoretical models, the response of a parent that is deserted should be different from that of a parent whose partner is present but not providing care (McNamara *et al.*, 2003; Houston *et al.*, 2005). Since Houston *et al.*'s review, several experimental studies have indeed combined these two methods (e.g., Lendvai *et al.*, 2009; Suzuki & Nagano, 2009).

Empirical results: biparental care

Negotiation models predict parents to partially compensate for a change in the amount of care provided by their partner in the case of biparental care (McNamara *et al.*, 1999; Akçay & Roughgarden, 2009). Several studies have provided results consistent with this prediction. For example, testosterone implants in male house sparrows led to a decrease in incubation effort of these males, which their female partners partially compensated for (Schwagmeyer *et al.*, 2008). Lendvai *et al.* (2009) also reported female house sparrows partially compensating for an experimental decrease in their partner's feeding effort. Experimentally increasing the amount of care during incubation in the Kentish plover also led to partial compensation by its partner (Kosztolányi *et al.*, 2009).

A detailed meta-analysis by Harrison *et al.* (2009) analysed 54 studies (ranging from the 1980s up to 2008) that investigated the response to reduced parental care by the partner in birds. They concluded that when the partner reduces its amount of parental care, either in terms of feeding behaviour or incubation behaviour, partial compensation indeed is the mean response, supporting the evolutionarily stable response that is predicted by negotiation models. They also found a difference between the sexes in their response, with females on average compensating more than males.

Although partial compensation seems to be the norm, results of experiments are not fully consistent (Harrison *et al.*, 2009; Houston *et al.*, 2005; Hill *et al.*, 2011; Johnstone & Hinde, 2006). Partners of manipulated parents have been reported to respond with full compensation, no compensation (i.e. lack of any response), and even matching, thus

covering all possible responses that were outlined previously. Full compensation has been found in zebra finches for example, where males were provided with extra-pair copulation opportunity during the incubation period, which led to a decrease in their incubation effort (Hill *et al.*, 2011). Their female partners responded to this reduced effort by fully compensating. Suzuki and Nagano (2009) found a lack of any compensation in a study on burying beetles, *Nicrophorus quadripunctatus*. This is an interesting species that shows biparental care, and in this species, parents raise the brood on a carcass that is prepared by burying it and making it into a ball (Figure 3). When parents had been handicapped and thus spent less time on carrion maintenance (which is considered to be a form of parental care), their partner did not change the amount of time they spent on this (Suzuki & Nagano, 2009). Finally, in a study by Hinde (2006), begging playback was used to increase one of the parents' provisioning in great tits, *Parus major*, and the response of the partner was to also increase its provisioning effort in turn (matching). The hunger level of the chicks was not manipulated and could therefore not influence any of the results, indicating that the parent responded to its partner's work rate directly.

So although partial compensation seems to be the general response, many studies have also provided results that appear inconsistent with theoretical predictions.

Empirical results: desertion

According to theoretical models, if a parent decides to desert the brood entirely, its partner should respond by increasing its parental care by the maximum amount possible (Griggio & Pilastro, 2007; McNamara *et al.*, 2003). Negotiation causes parents to not provide their maximum level of care, to avoid being exploited by their partner. Therefore, the amount of care provided by a parent should increase after its mate is gone, and to a larger extent than would be predicted under the hypothesis of partial compensation. Several studies have indeed found results that are consistent with this prediction. In magnificent



Figure 3 A burying beetle and its brood. (Photo: Rick Williams)

frigatebirds, *Fregata magnificens*, females nearly doubled their feeding rate after their mate had left, and thereby fully compensated for their mate deserting them (Osorno & Székely, 2004). Griggio & Pilastro (2007) also found that both deserted male and female rock sparrows (*Petronia petronia*) increased their amount of care after being deserted, with females even overcompensating for the loss of their partner's care, while deserted males only partially compensated for the loss of care. And as I mentioned earlier, Czyz (2011) showed that desertion by a parent can also influence the decision of its partner whether to stay or desert in a population of penduline tits. While 50% of the females in the control group deserted their nest, experimentally removing male parents resulted in almost all female partners staying.

McNamara *et al.* (2003) predicted that young might in some cases be better off with just one parent instead of two, because a parent is expected to provide more care when there is no negotiation. Royle *et al.* (2002) found support for this in zebra finches (*Taeniopygia guttata*), in an experiment in which the amount of care given by a single parent to half the brood was compared with the amount of care given by both parents together to the entire brood. A parent caring alone for half the brood provided more care per offspring than both parents caring together (Figure 4), supporting the theoretical prediction by McNamara *et al.* (2003).

As I mentioned before, several studies have combined mate removal and handicapping, to study whether the response of a parent that is deserted is indeed different

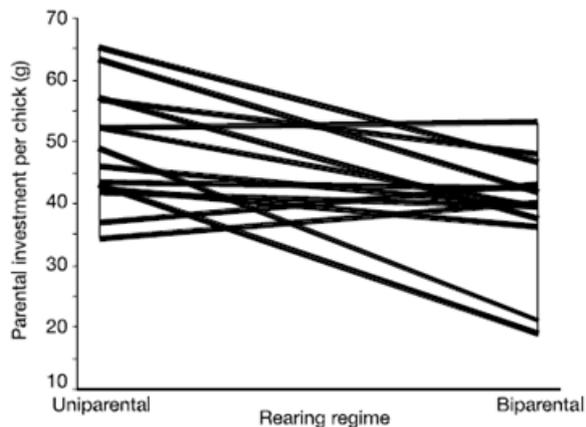


Figure 4 Parental investment per chick for uniparental and biparental rearing regimes. Lines represent individual females. Parental investment, measured as the amount of food consumed per chick, was greater for uniparental care. (from Royle *et al.*, 2002)

from that whose partner is present but not providing care, as has been predicted by theoretical work (McNamara *et al.*, 2003; Houston *et al.*, 2005). Suzuki & Nagano (2009) combined mate removal and handicapping in a study of burying beetles. As mentioned before, neither sex responded to handicapping of their partner, but after removal of their mate, males did increase their level of parental care, while females did not respond to mate removal. Smiseth *et al.* (2005) found similar responses to mate removal in the same species. The lack of response to a decrease in care by the partner could be caused by an inability of parents to assess the exact amount of care that is provided by their partner. Perhaps burying beetles are only able to assess whether their partner is present, but not how much care it provides when it is present.

Lendvai *et al.* (2009) combined mate removal and handicapping in house sparrows, and consistent with theoretical predictions, both manipulations led to an increase in parental care, with sparrows whose mate was removed increasing their feeding rate by a larger extent than sparrows whose mate was handicapped. Sparrows whose mate was removed thereby compensated fully for the lost care, while sparrows with a handicapped partner only showed partial compensation. Whittingham *et al.* (1994) also found results similar to this in a study on tree swallows (*Tachycineta bicolor*). The meta-analysis by Harrison *et al.* (2009) also supports the

theoretical prediction that birds that have been deserted by their partner should increase their feeding effort more than birds whose partners had been handicapped to only reduce their feeding effort (and thus were not removed entirely), although the mean response to mate removal was also partial compensation, and not full compensation. A possible explanation for this partial compensation could be that in some of these studies, the deserted parent did increase its care by the maximum amount possible, but this amount was still lower than the total amount of care that was provided by both parents together, thus resulting in partial compensation.

The empirical data for the response of a parent to its mate deserting seem to be mostly in line with theoretical predictions, with deserted parents increasing their amount of care by a large extent, and by a greater amount than parents whose mate is still present but has reduced its level of care.

3.3 Extended negotiation models

Several studies have extended on previously existing negotiation models in an attempt to explain the variety of responses that are found after a change in partner care, which are not in line with theoretical predictions. These models for example include the role of energy reserves (Barta *et al.*, 2002), and the amount of information that is available to each parent (Johnstone & Hinde, 2006).

Energy reserves

Barta *et al.* (2002) developed a state-dependent model that includes the energy reserves of both parents. Since parental care is costly, parents need sufficient energy reserves in order to successfully raise their young. Parents that have insufficient energy reserves may in turn abandon their brood. On the other hand, it has been suggested that a parent may also decide to abandon its current brood when its energy reserves are high, and the parent is therefore able to start a second breeding attempt within the same season (Barta *et al.*, 2002). In the model proposed by Barta *et al.*, a parent's decision about care provision depends on both its own energy reserves and that of its mate. A parent needs energy reserves above a

critical level to be able to provide care to its offspring. When a parent's level of energy reserves is too low to raise the young on its own, its mate will not desert because that would mean the failure of its current brood. When a parent's level of energy reserves is above the critical level for uniparental care however, its mate may decide to desert (Barta *et al.*, 2002).

An interesting consequence of the inclusion of energy reserves in Barta *et al.*'s model is that it provides parents with the opportunity to force their mate to care. A parent can strategically "handicap" itself by lowering its energy reserves to below the level required for uniparental care but above the level required for biparental care, thereby forcing its mate to stay and care as well (Barta *et al.*, 2002; Houston *et al.*, 2005; Osorno & Székely, 2004).

Osorno and Székely (2004) found that female frigatebirds from biparental broods had lower body reserves than females that were providing care alone, which is consistent with the predictions from the model by Barta *et al.* (2002). Similarly, Eldegard and Sonerud (2009) found that desertion rate was higher for Tengmalm's owls (*Aegolius funereus*) when food abundance and body reserves were higher. Eldegard and Sonerud also incorporated the effect of the mate's body reserves, and desertion was also higher with increased body reserves of their mate.

So interactions between parents seem to involve assessment of the partner's body reserves as well, since whether parents decide to desert or care seems to be influenced by the body condition of both parents. It is important to realise though that Barta *et al.* assume that parents are indeed able to accurately assess their partner's energy reserves, which needs further empirical support. Also, the model might not predict patterns of care for small birds that naturally show variation in their energy reserves throughout the day and that consequently hardly have the possibility to strategically vary their level of energy reserves.

The availability of information on brood need

Johnstone and Hinde (2006) extended on the model by McNamara *et al.* (1999; 2003) by including the amount of information each parent has on brood value or need. Their model focuses on two effects. The first is the availability of information regarding brood need or value, with an increase in care leading to an increase by its partner (i.e. matching) if each parent only has partial information, since an increase by one parent will serve as a signal of brood need to the other. The second is the marginal value of investment, with an increase in care by one parent leading to a decrease in care by its partner (because investment is assumed to yield decelerating returns). The strength of these two effects determines the exact response of a parent to a decrease in care by its partner, with information received from the partner's behaviour favouring matching of parental care, and the marginal value of investment favouring compensation (Johnstone & Hinde, 2006). The model predicts that if each parent can very accurately assess brood need, they will respond to a change in their partner's effort with partial compensation, as was also predicted by earlier models (McNamara *et al.*, 1999; Houston *et al.*, 2005). If each parent only has partial information regarding brood need however, they will interpret a change in care by their partner as a signal of a change in brood need, and this will lead to a matching response (Johnstone & Hinde, 2006). A theoretical study by Akçay and Roughgarden (2009) found similar results regarding the exchange of information between parents and the associated responses to a change in partner effort.

Incorporating the amount of information each parent has on brood need can therefore provide us with an explanation for the variety of responses to a change in partner care that are found, including matching (Hinde, 2006), while previous models by McNamara *et al.* (1999, 2003) did not explain these responses. However, the role of information on brood need in determining the response to a change in partner care still remains to be tested empirically.

Discussion

Sexual conflict over parental care is a topic that has been receiving a lot of interest for quite a while. Factors such as paternity and remating opportunities have already for a longer time been suggested to play a role in care patterns. Remating opportunities indeed appear to play an important role in how much care each parent provides to its young, while there does not seem to be a general pattern for paternity and the amount of care that is provided. However, parents are not only influenced by factors such as these, but by the behaviour of their partner as well. Therefore, when studying the amount of care that a parent chooses to provide, it is very important to also include the partner's behaviour, since this has been proven to influence how much the other parent cares (e.g., McNamara *et al.*, 2002; Houston *et al.*, 2005). Including behavioural interactions between parents is necessary to understand the decisions parents make within a single breeding season, as opposed to the parental care patterns shaped over evolutionary time. During the last decade or so, this behavioural interaction, or negotiation, between parents has been acknowledged as being an important factor in determining how much care a parent provides. This inclusion of negotiation between the parents into theoretical models has been one of the most recent developments in the study of sexual conflict over parental care.

Mismatch between theory and empirical data

Empirical data for the response of a parent to being deserted by its partner seems to support the theoretical prediction that deserted parents increase their care effort, and by a larger extent than parents whose mate has only reduced its level of care (without deserting entirely). However, studies on the response of a parent to their partner reducing its amount of care while still being present have not provided results in line with theoretical predictions. Although partial compensation, which is the response predicted by theoretical models in this case, seems to be the general response (Harrison *et al.*, 2009), the responses vary from full compensation to no compensation, and even matching has been found. So there is a lack of a consistent match

between theory and empirical data for the response of a parent to a change in its partner's effort. An intriguing question that remains is why this mismatch exists.

The mismatch might occur because current models are insufficient and additional factors (e.g. energy reserves, information on brood need) actually play a role in sexual conflict over care, or it might occur because the experimental methods used are not optimal. One example of the latter was proposed by Hinde (2006). In case of handicapping experiments, weighting and feather cutting can change the partner's appearance, and thus the assessment of its parental quality. The partner of a handicapped parent might not increase its care effort in response to a reduction in care by the handicapped parent, because it assesses its partner's quality as being lower, and therefore the chicks have a lower reproductive value as well. This could explain why several studies have found no response to a change in care effort by the partner. The type of parental care that is studied might also influence the response that is found. The meta-analysis by Harrison *et al.* (2009) revealed that the response to a change in the partner's effort was greater for feeding behaviour than for incubation behaviour. This might be explained by a reduction in feeding behaviour having greater costs (e.g. death of offspring) than a reduction in incubation behaviour (e.g. delayed development of offspring).

Difference in response between the sexes

Another factor that seems to play a role in the response to a change in partner's care effort is the sex that we are focusing on. There appears to be a difference in the response between the sexes, with most often females compensating more for a reduction in effort of their partner than males (Harrison *et al.*, 2009), though several studies have also reported the opposite effect, with males compensating more than females (Suzuki & Nagano, 2009; Harrison *et al.*, 2009).

One explanation for a difference in response between the sexes involves asymmetries in costs and benefits of parental

care. Costs of reproduction are generally assumed to be higher for females than for males, since females have to produce the eggs and often incubate the eggs on their own (Griggio & Pilastro, 2007; Trivers, 1972). Because of these high costs of reproduction, investment of a female in her current brood reduces the investment she is able to put into future broods. This reduced future reproduction, in combination with females often also having lower survival rates than males, might make it more beneficial for females to invest in their current brood, leading to relatively more compensation by females.

Johnstone and Hinde (2006) proposed informational asymmetry as another explanation for the difference between the sexes. If the male and female parent differ in the amount of information they have on brood need, the parent that has more information is predicted to show more marked compensation by their model. The parent that is less informed will show weaker compensation or no response at all, or if the asymmetry is very great, matching can even occur. It is often assumed that females have more information on brood need because they often spend more time with the young (e.g., because only females are able to incubate in some species), and therefore most of the time females are also predicted to show stronger compensation (Johnstone & Hinde, 2006).

Future directions

How much care each parent decides to provide depends on remating opportunities, level of paternity (but only in certain cases), the amount of care that is provided by the partner, and perhaps also on other factors such as the amount of energy reserves of both parents (Barta *et al.*, 2002), and the amount of information each parent has on brood need (Johnstone & Hinde, 2006). However, additional empirical data is needed to provide sufficient support for these last two factors.

Other factors could potentially influence the amount of parental care each parent decides to provide as well. Studies should investigate when each factor plays a role, and how these factors might interact to

lead to different end results. Additional factors that might play a role include for example the timing of desertion, since the role of negotiation has been suggested to decrease over the course of the breeding season (Smiseth *et al.*, 2006). Interactions between parents and their offspring may also have an effect on negotiation between the parents. And recently, linking behavioural ecology with quantitative genetics has received attention in the study of parent-offspring conflict (Smiseth *et al.*, 2008). Integrating these two fields of research in the study of sexual conflict over care could also provide us with novel insights, because it allows us to include potentially heritable variation between individuals. Muller *et al.* (2007) have suggested another interesting way in which females might be able to “trick” their partner into staying (just like they might be able to do using energy reserves). Females could potentially manipulate their partner’s share of care through the deposition of hormones (e.g. testosterone) in the yolk of eggs (which in turn will influence the begging behaviour and development of the chicks). Other factors that might be of importance include the amount of care that is required by the young (e.g. whether they are precocial or altricial), and predation risk (with high predation risk favouring biparental care; Székely *et al.*, 2007). It would also be interesting for studies to vary the amount by which parental care is reduced in handicapping studies, to get an even better indication of how a parent responds to changes in its partner’s share of care.

Future research should focus on the reason behind the mismatch between theory and data. Perhaps taking other suggested factors into account might provide us with a better prediction of when we will find each pattern of care, and how a parent responds to a change in its partner’s share of parental care. Overall, negotiation between parents does explain why for example the amount of care provided by two parents together can be lower than that provided by one parent on its own, but negotiation models are not yet able to predict all the responses that are found to a change in partner care effort.

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