



Anniversary Essay

The parental investment models of Maynard Smith: a retrospective and prospective view

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In his paper 'Parental investment: a prospective analysis', Maynard Smith (1977, *Animal Behaviour*, **25**, 1–9) introduced a game-theoretic approach to understanding the evolution of parental behaviour and addressed the broad issue of which sex should provide care for the young. This paper was important in that it introduced the use of game theory to the analysis of parental care. It also stimulated empirical work on care. We identify progress that has been made since the publication of the paper. In particular, although Model 2 of Maynard Smith (1977) has been used in several textbooks to explain the evolution of care, subsequent work has shown that this model is not built on a consistent view of how parental care influences future reproductive success through its effect on the sex ratio. Several models incorporate a consistent account in which opportunities to remate after desertion emerge from the analysis, rather than being specified in advance. More generally, it is not possible to consider parental care in isolation from factors such as paternity, mating preferences and mate choice behaviour. We identify various theoretical and empirical issues in the area of parental care research that we believe deserve further study if our understanding of care decisions is to advance. Taken together, the landmark paper of Maynard Smith (1977) stimulated new theoretical and empirical studies in parental care research and led to new insights into the behavioural interactions between males and females.

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The aim of Maynard Smith (1977) was to understand how natural selection shapes patterns of parental care across species. He put his work in the context of two papers: Trivers (1972) and Dawkins & Carlisle (1976). Trivers (1972, page 139) defined parental investment as 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'.

Trivers (1972) has been very influential (over 8000 citations) and established the idea that parental care could be analysed in terms of the action of natural selection on males and females, but one aspect of his treatment was criticized. Although in general Trivers pointed out that a decision about parental care should be based on future reproductive success, he sometimes argued for an effect of previous levels of care on how a parent should behave. For example, Trivers (1972, page 146) claimed that if two parents differed in their level of investment in their young then the one that had invested less would be tempted to desert because it would lose

less if the young were abandoned by both parents, and so the other parent would be under pressure to stay with the young.

Dawkins & Carlisle (1976) pointed out that the correct basis for a decision is not past investment per se but the consequences of future investment. They made it clear that in some circumstances past investment influences the consequences of future investment and hence should be taken into account. Dawkins & Carlisle illustrated the wrong way to make a decision by using the example of the decision about whether to continue developing a supersonic aircraft. As they state, it is wrong to base the decision on the argument that past investment should not be wasted. Although the aircraft was not mentioned by name, the date of the article indicated that Dawkins & Carlisle had Concorde in mind. (Concorde began scheduled flights in the year that Dawkins & Carlisle's paper was published.) As a result the mistaken form of reasoning is known in the biological literature as the Concorde fallacy (e.g. Dawkins & Brockmann 1980; Sargent & Gross 1985). Economists know it as the sunk cost fallacy (Arkes & Blumer 1985).

Dawkins & Carlisle (1976) suggested that parental care should be analysed using the concept of an evolutionarily stable strategy (ESS). Maynard Smith (1977) took up this suggestion and presented three models to investigate parental care patterns.

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THE MODELS

Model 1

This model is based on a limited time available for breeding. Maynard Smith (1977) referred to this as a discrete breeding season. The success of a mated pair of animals depends on the care that they devote to their offspring. If neither parent cares then all the offspring die. Following Maynard Smith, we introduce the following notation:

V_1 = number of surviving young if one parent cares;

V_2 = number of surviving young if both parents care;

p = probability of mating with another partner if the first partner is deserted.

Now consider the decision of a paired male. If he stays with his mate and helps her to care for the young his success is V_2 .

If he deserts, Maynard Smith assumed 'for simplicity' that he helps the second female. Thus his success is $V_1 + pV_2$. So a male should desert if

$$V_1 + pV_2 > V_2$$

i.e. if

$$p > (V_2 - V_1)/V_2. \quad (1)$$

As Maynard Smith pointed out, the same analysis can be applied to a paired female.

Model 2

In Model 1, breeding success just depends on the level of parental care. In Model 2 it depends on both the female's investment in eggs and the subsequent level of parental care. During a discrete breeding season males and females choose between caring for their young or deserting them. A female that produces a large number of eggs is less able to care for them. Maynard Smith incorporated this idea by assuming that if a female is going to desert she lays W eggs, whereas if she is going to care she lays $w \leq W$ eggs. Let

P_2 = survival probability of eggs when cared for by both parents;

P_1 = survival probability of eggs when cared for by one parent;

P_0 = survival probability of eggs when not cared for (i.e. both parents desert).

If a male deserts, he has a probability p of mating again.

There are four possible patterns of parental care (both parents care, male cares & female deserts, male deserts & female cares, both parents desert). Maynard Smith showed that any one of them can be stable. Stability is established by showing that the male's behaviour is the best response to the behaviour of the female, and the female's behaviour is the best response to the behaviour of the male. This is the condition for a Nash equilibrium (e.g. Houston & McNamara 1999).

To illustrate this concept consider the case of care by both parents. Given care by the female, the male has to achieve a higher success by caring than by deserting. Maynard Smith gave the following condition for this:

$$wP_2 > wP_1(1 + p)$$

i.e.

$$P_2 > P_1(1 + p). \quad (2)$$

Given care by the male, the female has to achieve higher success by caring than by deserting which means that

$$wP_2 > WP_1. \quad (3)$$

Maynard Smith showed that for given parameter values there could be more than one stable pattern of care. In particular, care by both parents and desertion by both parents are alternatives, as are care by just the male (male-only care; Maynard Smith called this pattern 'stickleback') and care by just the female (female-only care; Maynard Smith called this pattern 'duck').

Model 3

Models 1 and 2 are based on a discrete breeding season. In contrast, Model 3 involves continuous breeding, with the payoff to a strategy being its rate of producing offspring that survive to independence. In contrast to Models 1 and 2, males and females decide on the duration of care that they provide. Maynard Smith analysed a case in which the expected number of surviving offspring as a function of the duration of care T is βT when one parent cares and $(\alpha + \beta)T$ when both parents care. He showed that when $\beta > \alpha$, so that both parents are less than twice as good as one parent, either male-only care or female-only care could be an ESS.

The Role of the Models

Maynard Smith (1977, page 1) said that his models 'have an obvious air of unreality when compared to the qualitative and verbal models discussed by Trivers. They have the corresponding advantage of forcing one to make one's assumption clearer. The purpose of mathematical formulation in this case is almost entirely to clarify the assumptions made; mathematical manipulation is minimal'. Our general impression is that the assumptions were not subjected to critical scrutiny for many years.

Maynard Smith (1977) was a landmark work in parental care research. It became a standard reference in empirical, theoretical and comparative studies of care. Model 2 is discussed in textbooks about parental care (Clutton-Brock 1991) and animal behaviour (e.g. Krebs & Davies 1987, 1991, 1993; Barnard 2004; Davies et al. 2012; but not in Alcock 1989, 1998 or Dugatkin 2009). While there was a consensus among researchers that the models were conceptually important, the views were divided about whether the models would stand the scrutiny of empirical tests.

THE EFFECT ON EMPIRICAL WORK

Ketterson & Nolan (1994) argued that experimental removal of one parent (usually the male) tests one of the key predictions of Model 2: biparental care should occur when the parents working together would produce more young than a single parent. Experimental manipulations tended to show that in birds, in which two parents normally rear the young, two parents are often more productive than a single parent (Wolf et al. 1988; Bart & Tornes 1989; Clutton-Brock 1991; Harrison et al. 2009); nevertheless, the difference between uniparental and biparental nests was often small or statistically nonsignificant.

Experimental removal (or manipulation by other methods such as hormonal treatment) of one parent, however, is fraught with problems. First, as a response to removal of its mate, the remaining parent tends to increase its parental effort (Wright & Cuthill 1989; Harrison et al. 2009), thus changing the value of uniparental care. Second, Birkhead & Møller (1992) criticized experimental studies by saying that evidence from male removal studies may not be used to test the predictions of Model 2, since the value of biparental versus uniparental care can only be evaluated if widowed parents do not suffer any reduction in survival or future reproduction. Third, Clutton-Brock (1991) criticized the logical foundations of testing an ESS model in contemporary species. He argued that the results of such a test do not tell us much about the initial conditions

because care and life history have become coadapted as the care patterns have evolved since the ancestral condition. It is true that such an investigation does not establish the evolutionary origin, but it can show that current behaviour is evolutionarily stable. Furthermore, using experimental data (e.g. Harrison et al. 2009) and modern comparative methods one can infer past events, and thus reconstruct the ancestral conditions and test the directionality of selection using experimentally estimated fitness implications of male care, female care, biparental care and no care. As far as we are aware, reconstructing ancestral conditions using experimental data has not been done.

Clutton-Brock (1991) suggested that empirical investigations should concentrate on species that exhibit different types of care within the same population, for instance either the male or the female might care for the young. For example, in the Eurasian penduline tit, *Remiz pendulinus*, one parent (either the male or the female) provides full care on its own, incubating the eggs and rearing the young to independence. Since female-only care is more common than male-only care in all penduline tit populations that have been studied to date (van Dijk et al. 2010), one might expect females to be better parents than males. However, in a comparison of the reproductive success of female-raised versus male-raised families, there was no difference in growth or survival per chick (Pogány et al. 2012), and thus postdesertion fitness differences between males and females (e.g. higher mating opportunity for males) may favour male desertion.

While we agree with Ketterson & Nolan (1994) that experimental validation of theoretical models is an essential component of scientific progress, we note the striking gaps in experimental tests of the models of Maynard Smith (1977). First, few researchers have investigated the assumptions of the models, and asked whether his/her empirical system would fit the requirements of the models. For example, Models 1 and 2 assume discrete breeding seasons with the environment staying identical throughout the full breeding season. A more severe assumption of these models is that only the males can remate (see below for discussion). Second, nearly all studies have focused on male involvement in biparental care, and attempted to evaluate the implications of male care for reproductive success by removing (or manipulating) males. There has been a shortage of tests assessing the conditions for both males and females in the remaining three ESSs (male-only care, female-only care and biparental desertion).

We conclude this section by raising the issue of whether the models of Maynard Smith are meant to be tested. Parker & Maynard Smith (1990) distinguished between general and specific models of behaviour. General models are designed to expose the logic of the explanation of a broad phenomenon (e.g. fighting or parental care). The generality of these models means that they do not apply to any particular situation (Maynard Smith 1982). If testable predictions for a particular species are desired, it is necessary to develop an appropriate specific model that can be parameterized. Broad predictions across species may be possible. For example, all else being equal, a larger value of P_1/P_2 in inequality 3 makes biparental care harder to justify, but comparisons at this level are difficult because all else might not be equal. For further discussion see Houston & McNamara (2002).

THEORETICAL IMPORTANCE

Maynard Smith's (1977) paper was important at the time that it was published for several reasons.

(1) It offered simple models to understand a complex social behaviour, parental care. Parental behaviour was reduced to a small number of components, and the conditions offered the possibility of quantitative tests.

(2) The models explained behaviour in terms of future expectations rather than previous investment (Trivers 1972), so avoiding the Concorde fallacy. Maynard Smith emphasized this by using 'prospective' in his title.

(3) It introduced a game-theoretic approach to understanding parental behaviour. This approach to behaviour was not that common at that time, although later became a standard approach in animal behaviour research.

(4) Model 2 established a general point: alternative patterns of care could be stable. For example either male-only care or female-only care can be alternative stable outcomes. This shows the importance of evolutionary history: 'so that the actual state of affairs now depends on the 'initial conditions' in an ancestral species of which we can know nothing except by inference' (Maynard Smith 1977, page 7). We emphasize that this is variation in possible end states of evolution; it does not explain variation within a population. In Model 2 remating probabilities are specified in advance. It then follows by a result of Selten (1980) for asymmetric games, that at any ESS all members of one sex must adopt the same behaviour. Below we describe mechanisms that can account for within-sex variation in behaviour.

(5) In Model 3 the solution of the game depends on the operational sex ratio (OSR), defined as the ratio of sexually active and available males to sexually active and available females. In the model, animals are not available while caring, so the OSR is determined by the time devoted to care by males and females. The model includes the constraint that males and females have the same rate of reproduction (the Fisher condition). The requirement imposes a balance condition on the time for which members of each sex have to search for a mate. Thus the OSR depends on the behaviour of population members, and the behaviour of population members depends on the OSR. In other words, at evolutionary stability there is a consistent relationship between behaviour and OSR. The balance condition on the time that members of each sex have to search for a mate is widely used in models of care and sexual competition (e.g. Grafen & Sibly 1978; Clutton-Brock & Parker 1992; Yamamura & Tsuji 1993; Houston & McNamara 2002; Kokko & Jennions 2008).

Problems with Model 2

We focus on Model 2, which is what textbooks have done. It is also the model that Maynard Smith (1982) extended. We discuss a major limitation of this model: the lack of self-consistency.

Maynard Smith (1977) assumed that if a female is going to desert she lays W eggs, whereas if she is going to care she lays $w \leq W$ eggs. We find this assumption rather strange in that the female's choice of egg number constrains her pattern of care. This means that the female really makes only one decision.

A general problem with Maynard Smith's approach is that males have the chance to have a second breeding attempt in a season whereas females only have one (Székely et al. 1996). It is also difficult to provide a biological justification of the payoff to males. To illustrate this assume that a female cares for the young and ask whether a male should provide care or desert. Maynard Smith said that a male will care if condition (2) is met i.e. $P_2 > P_1(1 + p)$. This condition is based on the assumption that the male will not provide care in his second breeding attempt. Given the assumptions of the model, this does not seem plausible. If the second attempt is the last one in the season then the male should provide care (cf. Maynard Smith Model 1). If the male cares in the second attempt the condition for the male to care in the first attempt becomes

$$P_2 > P_1 + pP_2. \quad (4)$$

If the second attempt is not the last one, then the expression for the benefit of deserting in the first breeding attempt needs to take account of these subsequent attempts. Our conclusion is that it is hard to give a plausible biological account of mating behaviour that can justify condition (2).

Maynard Smith (1982) extended Model 2 to allow a male's probability of remating to depend on whether he cares or deserts. This does not make it any easier to give a coherent account, and introduces further problems. For example, assume that females care. Maynard Smith stated that the payoff to a male that cares is

$$wP_2(1 + p') \quad (5)$$

where p' is the male's probability of getting a second mating if he cares for the offspring from the first mating. This expression is based on the male helping his first female to care, then deserting her and finding another female that he will help. If instead the male had remained with his first female, he would presumably have a greater payoff of $2wP_2$. This possibility can only be eliminated by assuming that although a male can care twice in a season, a female cannot. Note that if the pool of females available for mating contains some females that have not already cared for young, then a male has the chance of pairing with such a female and she will produce a clutch size W rather than w .

These problems led Webb et al. (1999) to develop a consistent account of the payoffs to males and females.

Subsequent Theoretical Developments

We now describe four subsequent theoretical developments. The first two were introduced by Webb et al. (1999).

(1) Consistency. Webb et al. (1999) considered a two-stage model based on a single breeding season. If an individual cares then it only has time for one brood, whereas if it deserts it has the chance to have a second brood. Males and females decide whether to care for a brood or desert it. Both males and females that have deserted have the chance to remate with members of the opposite sex that have also deserted. This means that remating probabilities depend on the numbers of males and females that desert. Working back in time from the last brood in the season, Webb et al. found the evolutionarily stable patterns of care. In contrast to Maynard Smith (1977), remating probabilities are not fixed but emerge from behaviour. Thus the result of Selten (1980) no longer applies, and it is possible to have more than one care behaviour by members of a given sex at evolutionary stability. This provides a possible explanation of variation within a population, for example the coexistence of several patterns of care.

A key feature of the model is that the probability that an individual remates is not a fixed parameter. Instead it emerges from the behaviour of the whole population in a consistent way. As Webb et al. (1999, page 989) said 'a parental care pattern can be an ESS only if it is stable given the mating system that it generates'.

The importance of consistency and remating feedback is now widely recognized (Houston & McNamara 2005; Fromhage et al. 2007; Kokko & Jennions 2008; Alonzo 2010; Lehtonen & Kokko 2012; Lessells 2012). This feedback means that patterns of care are expected to depend on the OSR, a feature that was included in Model 3 of Maynard Smith but not in Model 2. In turn, the OSR is in part determined by the mating and parenting decisions of the animals themselves (Székely et al. 2000). Therefore, the OSR is as much a 'cause' as a 'consequence' of mating systems. Models need to provide a self-consistent account (McNamara et al. 2000; Kokko & Jennions 2008).

As we have pointed out, models indicate that the stable pattern of care depends on the probability of remating. It was initially

assumed that the mating probability was measured by the OSR. This led to attempts to demonstrate the effect of OSR on care, with mixed results (e.g. Breitwisch 1989; Balshine-Earn & Earn 1998; Liker et al. 2013). It is now realized that if individuals within a sex are different, for example some males are more attractive than others, there is no single remating probability (Cotar et al. 2008; Kokko & Jennions 2008; Lehtonen & Kokko 2012) and hence OSR is not adequate.

We can distinguish between two kinds of feedbacks (see also Klug et al. 2012).

(a) Feedbacks at an ecological timescale: courting, pair bonding and caring influence the number of individuals ready to mate in the population, and these, in turn, feed back to mating and caring decisions (Johnstone et al. 1996; Webb et al. 1999; McNamara et al. 2000; Kokko & Johnstone 2002; Houston et al. 2005; Kokko & Jennions 2008; Alonzo 2010). Therefore, to understand components of sex roles and breeding strategies, one needs to consider the reproductive decisions of all individuals in the population, including the ones that are not actually breeding at a given time.

(b) Feedbacks at evolutionary timescales. For example, the analysis of the evolution of the sex ratio provided by Fisher (1930) rests on noting that the rarer sex is at an advantage. When one sex is at an advantage we would expect selection to act on the sex ratio so that this advantage is reduced.

(2) Individual differences. Webb et al. (1999) showed how individual differences can result in a mixed-strategy ESS, and hence provide another explanation of several patterns of care within a population. This theoretical possibility has been used to analyse care in the penduline tit. This small passerine bird is highly polygamous (up to five mates in a single breeding season), and only one parent (the male or female) incubates the eggs and rears the young (Szentirmai et al. 2007). In addition, about 30–40% of clutches are deserted by both parents, and these clutches produce no young. This is remarkable, since the antagonistic interests of males and females appear to reduce substantially the productivity of penduline tits: biparental desertion is a more common source of nest failure than all other causes combined (e.g. predation, storms). An experiment in which eggs that had been cared for by one parent and eggs that had been deserted by both parents were artificially incubated found no difference in viability of cared for and deserted eggs (Á. Pogány, A. Kosztolányi, Á. Miklósi, J. Komdeur & T. Székely, unpublished data).

Using data from a Hungarian population of penduline tits, van Dijk et al. (2012) estimated the average seasonal reproductive success of males and females given their decision in their first breeding attempt. These population averages suggest that there are two alternative ESSs, female-only and male-only care. This does not agree with the observed patterns of care, in particular the fact that desertion by both parents is frequent. van Dijk et al. argued that the population averages are an inadequate basis for a model because they ignore individual differences in payoffs. They went on to show that a model in which males differ in attractiveness can account for the data. Like the population-level analysis, the latter model involves a single decision and hence is probably unrealistic. McNamara et al. (2002) argued that patterns of parental care do not emerge in this species as a consequence of independent decisions by each parent. In line with this argument, van Dijk et al. pointed out that parents may interact repeatedly before deciding whether they will care or desert.

(3) State and time. In many species, reproduction occurs in a well-defined breeding season. Webb et al. (1999) assumed that there were two distinct stages. In reality, the timing of breeding across a population is unlikely to be synchronized. McNamara et al. (2000) considered a dynamic model in which breeding can start at any time during the season and the numbers of unpaired males and females is determined by the care decisions of males and females.

At evolutionary stability, oscillations in the OSR select for periodic changes in the pattern of care over the breeding season. These periodic changes maintain the oscillations in the OSR.

The decision that an animal makes about care will have consequences for the energy that is used and the time spent with the young. It is therefore important to be explicit about changes in energy reserves in modelling parental care. Barta et al. (2002) showed that incorporating the effect of reserves can totally change the pattern of care and lead to counterintuitive outcomes. In particular, a parent may handicap itself by reducing its energy reserves in order to force its partner to care. We believe that experimental assessment of Barta et al.'s predictions can provide novel insight into the behavioural interactions between parents in biparentally caring species.

(4) The process of decision making. When Maynard Smith was developing his game-theoretic models, the standard assumption (often implicit) was that each individual made a single decision in ignorance of the decision made by its partner. This is often referred to as simultaneous choice. This assumption of no information will often be unrealistic, and various models have abandoned it.

The simplest of these models assume that a decision by members of one sex provides information to members of the other sex when making their decisions. For example, Kokko (1999) assumed that a female decides whether to offer extrapair copulations. Her partner then has incomplete information on his loss of paternity and adjusts his parental care accordingly. The effect of the order in which decisions about care versus desertion are made has been investigated by McNamara et al. (2003). (For a general account of whether it is advantageous to obtain information in games, see McNamara et al. 2006.)

Maynard Smith (1977), Yamamura & Tsuji (1993), Webb et al. (1999) and others modelled actions as simply 'desert' or 'care' (see also Lessells 2012). However, whether an individual cares or deserts is liable to be the result of following a rule that chooses one of these actions as a function of circumstances. It is important to view selection as acting on rules for choosing actions rather than on actions themselves (McNamara et al. 1999; McNamara, 2013). Rules involving negotiation of effort by parents and their young have been investigated by Johnstone & Hinde (2006; see also Johnstone 2011). This work makes it possible to predict how parents will react to each other. McNamara et al. (1999) showed that the evolutionarily stable negotiation rule can result in a lower level of care than the evolutionarily stable actions.

THE FUTURE

Various issues in parental care research deserve further study if our understanding of care decisions is to advance. Some issues are empirical, some are theoretical, some are both.

Empirical Work on Diverse Groups of Organisms

Much of the work on parental care has focused on birds, mammals and fish; there is a scarcity of studies in insects, molluscs and amphibians even though these groups harbour striking examples of care (McGraw et al. 2010). For instance, marine invertebrates exhibit great diversity in breeding systems (Kamel & Grosberg 2012). A marine snail *Solenosteira macrospira* presents a remarkably different scenario from the traditional subjects of parental care research in that females oviposit exclusively on shells of conspecific males, and the males carry eggs that are fertilized by up to 20 different males. Parental care is costly as shown by the reduced body mass of caring males. Thus it seems that males work hard to rear somebody else's offspring. Intriguingly, while the embryos develop inside the egg capsules they often devour their

siblings in a way that somehow favours the hatching of the caring males' own offspring (Kamel & Grosberg 2012). Further study of marine invertebrates and molluscs is likely to provide additional tests of existing theory, and may lead to new theoretical work.

Empirical Work on Process

The process by which individuals decide their level of care is crucial to the predicted level of care that evolves. Predictions depend on the extent of information that each parent gains about the other (see below), and on outside contingencies, such as the nearby presence of an alternative mate. Schwagmeyer et al. (2008) investigated interactions between parents and Meade et al. (2011) investigated interactions between parents and young in the context of negotiation, although further work is needed both in biparental species to understand male–female interactions and in uniparental species to understand the interactions between mated pairs and the rest of the population. Such studies may be particularly rewarding in species that exhibit different care patterns in the same population such as the Eurasian penduline tit.

Theoretical and Empirical Work on Learning and Coordination between Parents

Biparental care of the young is a taxonomically widespread behaviour that is present in numerous insects (e.g. cockroaches, burying beetles), fishes, frogs, birds and mammals including primates (Reynolds et al. 2002). While recent studies have provided important new insights into the neuroendocrinology and behavioural ecology of pair bonding and biparental care (Adkins-Regan 2005; Houston et al. 2005; McGraw et al. 2010), the role of learning in parental interactions has received much less attention. Offspring may learn parental roles while they are raised by their parent(s): maltreated chicks in Nazca boobies, *Sula granti*, maltreat their own offspring as adults (Müller et al. 2011). Furthermore, in biparental species one parent may watch the other parent's behaviour, and modify its own behaviour accordingly. Adjustments in behaviour as a result of learning about the mate's willingness to care for or protect the young can lead to either a stable and long-term pair bond with both parents caring or to the breakdown of cooperation and the pair splitting up. In the common murre, *Uria aalge*, a poor level of care by one parent can result in the other parent seeking a new mate (Moody et al. 2005).

Coordination of parental activities between the male and female parents is another rarely studied element of biparental care. *Ranitomeya imitator*, a poison dart frog, exhibits biparental care: the male surveys the pools in which the tadpoles develop, and at approximately weekly periods when food is running out, he calls the female to lay trophic eggs to supply the developing tadpoles. The coordination between the male checking the pond that contains the offspring, and the female's willingness to produce trophic eggs is essential for successfully raising any young (Brown et al. 2010).

Causal and Functional Approaches should be Linked

McNamara & Houston (2009) argued that rather than seeing causal and functional accounts as separate, they can be linked by considering the evolution of mechanisms. We suggest that pair bonds and parental care can be fruitfully viewed from this perspective. There is a growing realization among evolutionary biologists, developmental biologists and neuroscientists that in order to fully understand complex traits such as parental care, it is essential to use and combine both causal and functional approaches (Clutton-Brock 1991; McGraw et al. 2010; Royle et al. 2012).

Theoretical Work: Care is Multidimensional

Parents protect, defend and nurture their young in a variety of ways (Clutton-Brock 1991). These different components may not evolve together (Lessells 2012; Smiseth et al. 2012): a parent's involvement in one form of care may be independent from its involvement in another form of care. For instance, in a phylogenetic analysis of 400 bird species, the male's participation in chick brooding was highly correlated with his participation in incubation, although chick brooding was unrelated to postfledging feeding (Székely et al. 2013). As Houston et al. (2005) argued, models of parental care need to be extended to include the fact that care can vary along more than one dimension. Such models could be used to establish conditions for males and females to differ in the types of care that they provide.

Theoretical Work: Consistency is Needed at Many Levels

So far we have emphasized consistency within the context of remating probabilities. Even here there are additional complications. For example, if there are differential mortality risks associated with different care options (Kokko & Jennions 2008), then the OSR will depend on the strategy adopted by the population, and if the strategy depends on the OSR, consistency is needed.

Webb et al. (1999) assumed remating occurs only with unmated individuals. But males may also desert to gain extrapair copulations with mated females. If so, we must take into account the probability of mating with mated as opposed to unmated females (Fromhage et al. 2007), the resulting loss of paternity of mated males, and the effect of loss of paternity on male effort (included in models of Kokko 1999 and Liedtke & Fromhage 2012). It is then necessary to ensure consistency in both remating probabilities and in paternity: every offspring has to have precisely one mother and one father (Fisher 1930; Queller 1997).

It may, however, not be sufficient to take the rate of extrapair copulations as a given parameter. Why would females give extrapair copulations and what processes result in differential paternity? Are there differences between males? If males or females are different, the range of types needs to be explicitly included in models. The balance equation for remating and paternity consistency still applies overall when there are different classes of male, but not necessarily within classes (e.g. Webb et al. 1999; Houston & McNamara, 2002). For example, a high-quality male might lose little paternity to rival males and gain a lot by mating with their females. The details may matter here. In evaluating the advantage of giving extrapair copulations, the effect on care by the social male may have to be factored in. A complete model should be able to predict rates of extrapair copulations from the range of male types and other aspects of the system. In their study of the ocellated wrasse, *Symphodus ocellatus*, Alonzo & Heckman (2010) found an increase in paternal care with increasing intensity of sperm competition. This result presents a challenge to models that attempt to predict how the level of care depends on paternity. As Alonzo & Heckman suggested, it is probably necessary to include dynamic interactions between parental males, sneaking males and females.

There are also liable to be differences between females. Differences between members of a sex raise the possibility that individuals are not choosing their partners at random from those available. If there is active choice, then predictions are changed since now an individual that deserts is not deserting a randomly selected partner but one that was actively chosen for certain qualities.

Preferences for males are probably affected by the value of the potential partner, for example whether he is liable to care.

However, whether a partner is liable to care will depend on his remating probabilities and hence on the preferences of the opposite sex (Cotar et al. 2008); self-consistency is again required.

Mate choice is more likely to be a process rather than a single decision. For example, in McNamara et al. (2009) males are either helpful or nonhelpful. When a female encounters a male she inspects him to obtain information about his type. The inspection ends either when the female decides to mate with the male, or when she rejects him and starts searching for another male. Prolonged inspection corresponds to coyness. The optimal level of coyness depends on variation in types in the population. The range of types is subject to evolution. Again consistency is required.

CONCLUSIONS

Natural selection will favour the action that maximizes current reproductive success plus future reproductive success (Williams 1966). In the context of parental care it is relatively easy to model the effect of parental behaviour on the success of the current breeding attempt. Maynard Smith (1977) was clear that it was necessary to incorporate future reproductive success, and he presented three models of care that initiated the game-theoretic approach to care.

However, his models have shortcomings. One general problem was that males and females were treated in a fundamentally different fashion in that males were given the opportunity to remate but females were not. As we have pointed out there were also specific problems with how remating was represented. Instead of capturing future consequences of female care in terms of remating, Maynard Smith introduced a link between the number of young produced by a female and her pattern of care. His assumption is that if a female is going to care she lays fewer eggs. It seems more reasonable to capture the idea of a cost of care in terms of a deterioration in the female's state after care. Maynard Smith's assumption means that the number of eggs a female lays provides the male with information about her pattern of care.

Maynard Smith addressed the broad issue of which sex should provide care for the young. After over 30 years of work, we have a much better understanding of the interaction between care and other aspects of reproduction. Along the way we have realized that parental care can be investigated on a finer scale than was provided by Maynard Smith. Thus instead of just asking which sex should care, we can ask how an individual's state and the time in the breeding season should influence its decisions.

Science often makes progress by breaking a complex system into simple components that can be analysed in isolation. For example, Houston (1990) pointed out that a complete account of parents feeding their young would involve game-theoretic interactions between the parents and also between the parents and the young (Parker et al. 2002). It might be possible to make some progress by analysing one of these games while ignoring the other, and also ignoring the details of how the parents forage. It also might be possible to understand the economics of how the parents forage without analysing the various game-theoretic interactions (e.g. Orians & Pearson 1979; Houston 1987). A fundamental message that emerges from work since Maynard Smith (1977) is that in the context of parental care everything interacts with everything else.

A full model of parental care should be put in the context of life history and ecology, and ultimately have the OSR, extrapair copulations and paternity, mating preferences, mate choice behaviour and care behaviour emerge in a holistic and consistent manner. Although there has been progress on linking some of these topics (e.g. Johnstone et al. 1996; Parker & Simmons 1996; Houston & McNamara 2002; Kokko & Johnstone 2002; Kokko & Jennions 2008; Alonzo 2012; Lessells 2012; Klug et al. 2013a, b), as far as

we can tell, no model investigates all the relevant aspects. All models need to make simplifications, but it is important to decide what components can be ignored. Given the importance of consistent accounts of remating and paternity for understanding parental care, these features deserve to be included.

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