THE ROYAL SOCIETY

Relating paternity to paternal care

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Intuition suggests, to most people, that parents should be selected to care for their offspring in relation to how certain they are of being the parents of those offspring. Theoretical models of the relationship between parental investment and certainty of parentage predict the two to be related only when some other assumptions are made, few of which can be taken for granted. I briefly review the models and their assumptions, and discuss two kinds of difficulty facing an empiricist wishing to test the models. The first is the problem of unmeasured (and immeasurable) variables. The second is the problem that even the most extensive models do not capture the complexity that can be demonstrated in real systems. I illustrate some of these problems, and some qualitative tests of the models, with experimental work on a population of the collared flycatcher. My conclusion is that although there are some cases where the models have qualitative support, we are a long way from understanding whether paternal care is commonly adjusted in relation to certainty of paternity.

Keywords: relatedness; parental investment; optimality; trade-off

1. INTRODUCTION

The application of genetic markers to study parentage has become widespread since the first use of these techniques in the 1980s (e.g. Burke & Bruford 1987; Wetton *et al.* 1987; Avise 1994; Birkhead & Møller 1998). The discovery of great variation both between and within species in the relatedness of parents to their offspring has increased the relevance of the question of how parentage should be related to parental care. This question has a relatively long history. Trivers (1972) suggested that parental investment should be related to certainty of parentage, and explicit models of the relationship between parentage and parental care were constructed even before widespread evidence for variation in parentage became available (Dawkins & Carlisle 1976; Maynard Smith 1977; Grafen 1980; Werren *et al.* 1980). Initial models suggested that there should be no relationship between parentage and parental care, a conclusion which is at odds with that of those employing verbal arguments (e.g. Trivers 1972). More recent models have used differing (and broader) assumptions, and have shown that, under some circumstances, parentage can be expected to influence parental care (e.g. Winkler 1987; Whittingham *et al.* 1992; Xia 1992; Westneat & Sherman 1993; Houston 1995; Kokko 1999; Mauck *et al.* 1999). This is an area with an extensive and varied theoretical underpinning.

Many empirical studies have sought to test whether there is a relationship between parentage and parental care, with mixed results (e.g. Dixon *et al.* 1994; Wright & Cotton 1994; Westneat 1995; Sheldon *et al.* 1997; Sheldon & Ellegren 1998; Kempenaers *et al.* 1998), and there has been some discussion about which methods are most appropriate for tackling this question (Lessells 1994; Kempenaers & Sheldon 1997, 1998; Lifjeld *et al.* 1998; Wagner *et al.* 1998; Wright 1998). My aims in this paper are threefold. First, to briefly review models of how parentage should be related to parental care. Second, to explore the particular difficulties involved in translating the predictions of the models to tests of real organisms and third to illustrate these difficulties with some work conducted on a population of wild birds. From here on, I will refer to 'paternity' instead of 'parentage' and 'paternal care' instead of 'parental care', because it is much more often the case that males can be expected to be unsure of their parentage than can females. However, the terms can, in principle, be used interchangeably, and can thus represent situations in which females may be unsure of their parentage of offspring. In addition, much of the paper is written from the perspective of one studying this question in birds, which can be defended on the grounds that this area has been a particular focus for ornithologists, probably because of the high frequency of biparental care in birds. Of course, the problem is more general than this, and interesting work could be done on non-avian systems (e.g. Svensson *et al.* 1998).

2. TERMINOLOGY

One problem that has plagued studies of the relationship between paternity and paternal care is a confusion over what particular terms mean, and how they should be used (Westneat & Sherman 1993; Schwagmeyer & Mock 1993; Kempenaers & Sheldon 1997). For example, although it is commonplace (and I have followed the tradition) to discuss the relationship between paternity and paternal care, no model actually makes any prediction

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about the relationship between these two variables; nor could it do so. Evolutionary models predict how parental investment should respond to variable relatedness to offspring, where parental investment is defined as the decrease in parental reproductive value due to caring for offspring (Trivers 1972). However sophisticated the measures of parental care one makes are, there is no guarantee that they tell one anything about how much an individual is investing in a breeding attempt. This is, in part, because we have good reasons to expect individuals to differ in how much reproductive value they have available to spend on parental care (Van Noordwijk & De Jong 1986; Grafen 1989). Thus, a parental expenditure of 10 kJ h^{-1}, or a rate of feeding young of 25 caterpillars h^{-1}, may represent different amounts to different individuals. As a simple analogy, using indices of parental care as a substitute for parental investment is akin to using the absolute size of a person's telephone bill as an estimate of what proportion of their salary they spend on phone calls. Another reason for estimates of parental care to be weakly related to parental investment is that the costs of parental care may be paid far in advance (e.g. over winter (Nilsson & Svensson 1996)). Other events occurring between the end of parental care and the point at which the costs are incurred will tend to blur the relationship between care and investment. The only situation in which the use of parental care indices is defensible is when subjects have been randomized between experimental treatments. Thus, non-experimental studies cannot be used as a test of *models* of the relationship between paternity and paternal investment (Kempenaers & Sheldon 1997, 1998).

Further confusion has involved the way in which 'paternity' and 'certainty of paternity' should be used. While variation in paternity can cause selection on parental strategies, it may not be of relevance to the question of whether males adjust paternal investment facultatively in response to a hypothetical perception of their relatedness to offspring. This is of importance in the context of experimental manipulations which may seek to investigate the relationship between certainty of paternity and paternal care. An experiment might manipulate paternity (i.e. relatedness to the brood) but, if there were no cue available to males to indicate that relatedness had changed, we could not reasonably expect them to change their parental behaviour accordingly (Lifjeld *et al.* 1998*a*). Equally, an experiment might manipulate certainty of paternity, without manipulating paternity, and it could provide valuable evidence in support of a relationship between certainty of paternity and paternal care. If we could measure certainty of paternity and paternity for individuals, we should expect to find at least some correlation between the two, since if there is no link between the two any adjustment of behaviour in response to certainty of paternity cannot be correlated with the reproductive value of the brood. Interrelationships between paternity, certainty of paternity, paternal care and paternal investment are shown in figure 1. This figure suggests that one difficulty in exploring the relationship between paternal investment and certainty of paternity is that this is a relationship between two variables which cannot be measured directly, and for which we must employ surrogate variables which we assume are correlated with those of interest.

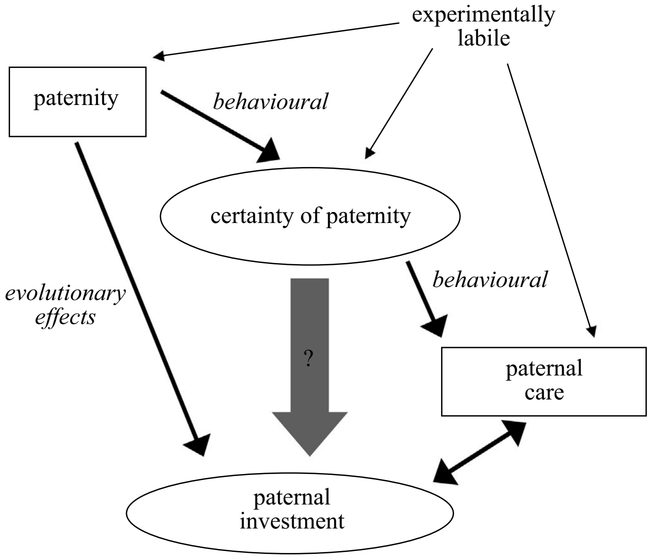

Figure 1. Interrelationship between paternity, certainty of paternity, paternal care and paternal investment. Variables in rectangular boxes can be measured directly, those in elliptical boxes cannot. The grey arrow indicates the relationship which models of facultative male response to variable certainty of paternity address. Paternity and paternal investment can, in principle, be linked via two pathways. There may be an evolutionary response of parental investment to mean relatedness to offspring. Alternatively, the linkage may be behavioural. It is this latter pathway which theoretical models have, largely, addressed.

3. SUMMARY OF MODELS

Reproducing animals face two major phenotypic trade-offs, which are widely thought to form the basis of the trade-offs that structure the evolution of life histories (Lessells 1991; Stearns 1992). These two trade-offs concern that between number and quality of offspring within a single breeding attempt, and that between current and future reproduction. If there is any relationship between certainty of paternity and paternal investment it comes about because of the second sort of trade-off. The value of a breeding attempt to a parent is determined by the number of offspring from that breeding attempt which survive and become successful breeders themselves. The effect of variable certainty of paternity is to affect the value of the current breeding attempt via changes to a male's expected relatedness to the offspring of that breeding attempt. However, the changed value of the current breeding attempt can only have consequences for a male's parental behaviour if there is a trade-off between the male's parental behaviour and his subsequent reproductive success (i.e. if the male's behaviour is actually parental investment). This follows because if how a male behaves does not impact on his future reproductive success, there is nothing to be gained or lost by following a particular behavioural rule in response to certainty of paternity. This simple reasoning immediately suggests that the framework under which one should try to assess the influence of paternity on paternal care is one based on life-history decisions. It also suggests, incidentally, that any effect of paternity on paternal care could only be expected in iteroparous breeders.

Some authors (e.g. Westneat & Sherman 1993) have

Table 1. Formal models of the effect of paternity on paternal care.
(Studies included in this table are restricted to those which have attempted to model the relationship between paternity and paternal care in biparental systems; see Sozou & Houston (1994) for more complex situations.)

reference	type of model	paternal investment related to certainty of paternity?
Maynard Smith (1977)	ESS	No
Grafen (1980)	marginal value	No
Werren *et al.* (1980)	ESS	sometimes
Winkler (1987)	static optimization	sometimes
Whittingham *et al.* (1992)	static optimization	sometimes
Xia (1992)	ESS	sometimes
Westneat & Sherman (1993)	static optimization	sometimes
Houston (1995)	static optimization	sometimes
Kokko (1999)	ESS	sometimes
Mauck *et al.* (1999)	dynamic programming	sometimes

Table 2. Relationships between parental care measures and measures of offspring fledging condition and recruitment for families of collared flycatchers.
(Data collected over four years, 1995–1998 (Sheldon *et al.* 1997; Sheldon & Ellegren 1998; B. C. Sheldon, unpublished data). Values are residual feeding rates correcting for year and date associated variation, as are fledging condition values (residual weight from general linear model with hatching date, year and tarsus length as predictor variables). Sample sizes differ because nestlings were not weighed in one year.)

measure of parental care	r	$b \pm$ s.e.	N	p
(a) fledging condition				
male rate of feeding	0.282	0.075 ± 0.021	113	<0.001
female rate of feeding	0.181	0.046 ± 0.028	113	0.11
male share of feeding	0.200	1.55 ± 0.73	113	0.04
(b) recruited offspring				
male rate of feeding	0.185	0.030 ± 0.012	152	0.015
female rate of feeding	0.002	0.000 ± 0.014	152	0.99
male share of feeding	0.205	0.975 ± 0.384	152	0.012

distinguished ‘mating effort’ from parental effort and ‘somatic effort’, where mating effort is effort expended trying to obtain more matings and somatic effort is effort expended on self-maintenance. I prefer to treat mating and somatic effort as one, since the only function of somatic effort is to survive to pursue more matings, albeit far in the future (see also Houston 1995).

Table 1 summarizes the main models that have made predictions about the relationship between paternity and paternal care, and draws on Table 1 in Westneat & Sherman (1993) for its general structure. As models have developed in sophistication, and increased the number and range of the variables that they treat, so, unsurprisingly, have their conclusions become broader in the sense of the range of outcomes that they predict. While early models (e.g. Maynard Smith 1977; Grafen 1980) concluded that paternity was unlikely to influence paternal care, it seems that this is because these papers made the assumption that parentage would be fixed for all matings that an individual made (Westneat & Sherman 1993). This assumption seems not to match observations from repeated mating attempts of individuals (e.g. Dixon *et al.* 1994; Freeman-Gallant 1996). All recent models predict that a relationship between certainty of paternity and paternal investment can occur, although its detectability may vary with life-history characteristics (e.g. Houston 1995; Mauck *et al.* 1999).

4. TRANSLATING MODELS TO REALITY

(a) *Comparative tests*

If a species is characterized by a high rate of extra-pair paternity, and males are commonly selected to reduce their level of parental investment in response to variable paternity, one might expect that over an evolutionary time-scale this species would evolve a lower *mean* rate of paternal investment than a species where extra-pair paternity is lower. The logic behind this argument is that if there exists genetic variation in the extent to which males are prepared to share parental investment with the female with which they breed, and if there are trade-offs between current and future reproduction, males that are genetically predisposed to care less for their offspring will tend to be more successful in the future. In contrast, those males genetically predisposed to provide a larger share of parental investment will tend to do so at the expense of rearing the offspring of less generous males. Thus, if one accepts that risks of extra-pair paternity, and sex differences in parental investment, are estimable (and in some way species specific), one can predict a negative relationship across species between the share of parental care performed by males and the rate of extra-pair paternity.

This comparison was first made for birds by Møller & Birkhead (1993), who found a significant negative relationship between measures of male parental care and extra-pair paternity across species; the relationship held when phylogenetic comparative methods were used. Some aspects of the analysis of Møller & Birkhead (1993) were disputed (Dale 1995; see Møller & Birkhead 1995), and a repeat of their analysis with a larger dataset found no association between rates of extra-pair paternity and male contributions to nestling care, although there was a negative relationship with the male's contribution to incubation (Schwagmeyer *et al.* 1999). Recent analyses with a further-expanded dataset again suggest a negative relationship between male contributions to parental care and rates of extra-pair paternity (K. E. Arnold & I. P. F. Owens, unpublished data; Møller & Cuervo 2000). Thus, there is some evidence in support of the suggestion that male parental care and extra-pair paternity covary in birds.

However, it is debatable whether the comparative analyses are at all relevant to the question of whether males adjust paternal investment in response to certainty of paternity. First, the evolutionary mechanism required to produce the association does not require any facultative change in parental behaviour on the part of males, and indeed it is not obvious that highly plastic parental behaviour is compatible with the evolution of a relationship between paternal care and rate of extra-pair paternity. Second, a relationship across species is no more evidence for a trade-off occurring at the level of individuals than is a relationship across individuals (Lessells 1991).

Third, and most tellingly, it is possible to explain the association between paternal care and extra-pair paternity in a different way, which reverses the causality of the relationship. Gowaty (1996) suggested that female birds were sometimes constrained in their ability to seek EPFs by the requirement of male assistance in rearing offspring. In species where male assistance was less necessary females would be more free to choose the genetic fathers of their offspring because the loss of male assistance with offspring would be less costly. This argument has been used to explain the exceptionally high rates of extra-pair paternity found in cooperatively breeding superb fairy wrens *Malarus cyaneus*. Rates of extra-group paternity are significantly higher when a group contains helpers which can potentially compensate for a reduction in care by the reproductive male (Mulder *et al.* 1994). Recent comparative analyses of the association between male parental care and extra-pair paternity support the model of Gowaty (1996) (Møller 2000; K. E. Arnold & I. P. F. Owens, unpublished data). In summary, while comparative analyses show that there are associations between paternal care and extra-pair paternity, it is hard to see any clear relevance of these associations to the question of whether males facultatively adjust paternal investment in response to variable certainty of paternity.

(**b**) *Empirical intraspecific tests*

Much of the work on the relationship between paternity and paternal care has been conducted on birds, and in this case, an avian bias is probably justified because more is known about parental care and parentage in wild birds than in any other class. Furthermore, birds are characterized by biparental care and variable parentage between species (e.g. Petrie & Kempenaers 1998). Several studies have approached the question of whether paternal care is adjusted in response to certainty of paternity by seeking correlations between non-manipulated measures of paternity and paternal care (e.g. Gavin & Bollinger 1985; Westneat 1988, 1995; Morton *et al.* 1990; Whittingham & Lifjeld 1995; Dunn & Cockburn 1996; Wagner *et al.* 1996). This is problematic on two counts. First, it seems unlikely that males can directly determine their paternity, as there is no evidence of an ability of birds to discriminate between maternal half-siblings (Kempenaers & Sheldon 1996). Thus, there is no sound basis for assuming that a male's genetic parentage bears a close relationship to his certainty of paternity. Second, models predicting a relationship between certainty of paternity and paternal care are based on trade-offs within individuals. They cannot be tested by measuring correlations across individuals, because it is unlikely that all individuals are subject to identical trade-offs (Lessells 1994; Kempenaers & Sheldon 1997, 1998). Correlational studies of paternity and paternal care are thus not appropriate for rejecting the models.

A more robust non-experimental means of testing for an association between certainty of paternity and paternal investment is, rather than looking at correlations across individuals, to use correlations within individuals (strictly speaking, in this case, within pairs). Restricting comparisons to those within a pair potentially controls for many confounding influences on levels of male parental care (Lessells 1994). This approach has been taken by two studies, both of which found positive relationships between changes in paternity and changes in measures of parental care (Dixon *et al.* 1994; Møller & Tegelström 1997). However, there are three difficulties with this approach. First, while restricting comparisons to pairs controls for much variation, it does not prevent the possibility that an association between paternity and paternal care is caused by a third variable with independent effects on the two, which fluctuates between breeding attempts. Second, as before, paternity is not the same as certainty of paternity. Finally, as Freeman-Gallant (1996) suggested, paternal care may be the target of female choice, in which case the causality is reversed.

Experimental tests of the relationship between certainty of paternity and paternal investment have produced mixed results. A wide range of different experimental techniques and study organisms have been used, making it difficult to combine the results of different experimental studies. Three experiments have used female detention to try to manipulate male certainty of paternity, of which two found effects on subsequent paternal care (Wright & Cotton 1994; Sheldon *et al.* 1997) and one did not (Kempenaers *et al.* 1998). Male detention or removal has been employed by seven studies, of which five have found effects on subsequent male care (Møller 1988; Davies *et al.* 1992; Lifjeld *et al.* 1998*b*; Sheldon & Ellegren 1998; Osorio-Beristain & Drummond 2001) and two have not (Whittingham *et al.* 1993; MacDougall-Shackleton & Robertson 1998). In the next section I synthesize a number of experiments which employed both approaches in the collared flycatcher *Ficedula albicollis*.

5. CERTAINTY OF PATERNITY AND parental effort IN THE COLLARED FLYCATCHER

A population of collared flycatchers breeding on the Swedish island of Gotland has been the subject of an intensive population study since 1980. Work on sexual selection in this population has been an increasing component of work since the early 1990s. As it was known that paternity varied among males (Sheldon *et al.* 1997*a*; Sheldon & Ellegren 1999), and that trade-offs between current and future reproduction affected both females (Gustafsson & Sutherland 1988) and males (Gustafsson *et al.* 1995), the species was well suited for the investigation of relationships between certainty of paternity and paternal effort. Furthermore, this species is relatively easy to capture (facilitating experimental manipulations) and it is easy to observe rates of parental provisioning. I conducted two different experimental studies which aimed to determine whether paternal effort was related to certainty of paternity (Sheldon *et al.* 1997*a*,*b*; Sheldon & Ellegren 1998); these involved attempting to manipulate certainty of paternity by experimentally removing females and males, respectively.

(**a**) *Female removal experiment*

Several behavioural studies of copulation in territorial birds have shown that females may control the occurrence of Eparental cares by visiting extra-pair males in their territories and copulating with them there (Kempenaers *et al.* 1992; Sheldon 1994*a*). These studies thus suggest that a possible cue for reduced paternity to a male would be the absence of the female from his territory, particularly at times when the female is fertile. Experimental and observational work (Davies *et al.* 1992; Sheldon 1994*b*; Hankinson 1999) suggests that males have some awareness of the fertility status of their mates, and particularly that the appearance of the first egg of the clutch in a nest acts as an important cue to female fertility. In this experiment we aimed to decrease a male's certainty of paternity by capturing female collared flycatchers as they entered the nest box to lay the second egg of the clutch (modal clutch size = 6). Experimental females (group E1; $N = 16$) were detained for 1 h and then released away from their territory, while control females (group C; $N = 17$) were released immediately after capture. A further manipulation was performed for a third group of females (E2; $N = 9$) which were captured on the morning that they laid both the second and fourth egg of the clutch, and detained for an hour in each case. As fertilization presumably occurs *ca.* 24 h before oviposition, any Eparental cares which occurred at the date relative to laying as the manipulation in E1 was conducted could potentially influence the paternity of the fourth and subsequent eggs. The further manipulation of females in the E2 group would, however, only be expected to influence certainty of paternity for the sixth and any subsequent eggs. Here I assume that a female's absence after a particular egg has been laid does not affect the certainty of paternity for previously laid eggs. This may not be correct.

As a measure of male parental effort, we recorded rates of parental provisioning to young aged 6 and 11 days for each pair; for males at least, feeding rates measured at these two ages were quite repeatable ($r = 0.72$, $p < 0.0001$ (Sheldon *et al.* 1997*b*)). The experimental treatment had a weak, but statistically significant effect on the share of feeding visits to the young made by the male. Males in E1 nests fed significantly less than males at C nests, although males at E2 nests fed at a rate intermediate between those at E1 and C nests. Combining the experimental groups (E1 + E2), males from these nests made a smaller share of feeding visits than males at control nests ($F_{1,37} = 5.495$, $p = 0.025$), and their rate of visiting the nest was significantly lower ($F_{1,37} = 4.744$, $p = 0.036$). Nestlings reared in the E1 group were in significantly poorer condition (residual fledging mass) than nestlings in the E2 group; the difference between E1 and C nestlings was marginally non-significant (Scheffe test, $p = 0.07$), although there was a significant positive relationship between the male share of feeds and nestling fledging condition ($F_{1,37} = 4.311$, $p = 0.039$; $\beta = 1.96 \pm 0.92$). Further details of the experimental results can be found in Sheldon *et al.* (1997*b*).

(**b**) *Male removal experiment*

This experiment was conducted as part of an investigation of the uses of mixed paternity broods for quantitative genetic studies in wild birds. Lifjeld *et al.* (1997) had shown that temporary experimental removal of male pied flycatchers (*F. hypoleuca*) increased the rate of extra-pair paternity dramatically, and I was interested in using this technique as a way of experimentally creating maternal half-sibling families (see Sheldon *et al.* (1997*a*) for further rationale). However, as a by-product this experimental technique created a group of males for which paternity had been experimentally reduced, and which therefore provided a complementary experimental manipulation to that described earlier (where female removal was used in an attempt to influence male certainty of paternity).

Males of experimental pairs were captured and transported to aviaries for 48 h when a complete nest had appeared in the nest-box that they defended. In some cases the removal was conducted on the day that the first egg of the clutch was laid, but otherwise the removal occurred a variable number of days (1–7) before the first egg was laid. The males were released near their nest box after 48 h, and in the majority of cases regained their territory (see Sheldon *et al.* 1999*a*). After clutches were complete, they were transferred to non-experimental nests, and observations of parental provisioning conducted at the experimental nests when young were 6 and 11 days old. Parentage analysis of the resulting broods revealed that the rate of extra-pair paternity was elevated in experimental families, and that the proportion of young sired by the male that had originally been removed was significantly related to the relative date of removal: males removed closer to egg laying fathered a greater proportion of the brood (Sheldon & Ellegren 1998; Sheldon *et al.* 1999*a*).

The rate at which males fed young, and the proportion of feeding visits that they made, were positively related to their share of paternity in the brood. The rate at which females fed the brood was, correspondingly, negatively related to their mate's share of paternity. As all males were feeding unrelated offspring, we could rule out the unlikely possibility that they were using discriminant cues (*sensu* Westneat & Sherman 1993) to determine their relatedness to the brood and feed the young accordingly. Thus, males must have had an indirect cue to their paternity in order to adjust their level of parental care accordingly. Since male paternity was strongly related to the date of removal relative to egg laying ($r_S = 0.56$, $n = 31$, $p = 0.001$), the date that they were removed provided a potential cue to males. Evidence that this was the cue that males were using is provided by the fact that when the relative date of the experimental removal was added to a model including male share of paternity, relative date of removal (rather than share of paternity) explained variation in male parental care (Sheldon & Ellegren 1998).

(c) *Costs and benefits of male parental care, and consequences for sexual selection*

The experimental studies described above (Sheldon *et al.* 1997*a*,*b*; Sheldon & Ellegren 1998) suggest that male collared flycatchers may adjust their parental investment to their certainty of paternity. At least, an experiment which was designed to mimic female behaviour while seeking Eparental cares resulted in a small reduction in the male's contribution to parental care. A rather different experiment, which substantially influenced the male's share of paternity, also resulted in correlated changes in male parental effort, although the experimental design suggests (because all males reared unrelated offspring) that again it was male certainty of paternity which provided the link between paternity and paternal effort.

Do these responses by males make sense? We can answer this question in fairly broad terms by considering what is known about costs and benefits of parental care in this population of collared flycatchers. Brood-size manipulations of collared flycatchers conducted over the course of the 20 year study of this population have revealed that experimentally increased parental care can influence several aspects of future reproductive success, particularly in females (Gustafsson & Sutherland 1988). For male collared flycatchers, elevated parental effort in one year does not influence probability of survival, or laying date or clutch size in the following year for those males that survive (*ca.* 45% of adults survive from one year to the next). However, three separate analyses have shown that experimental manipulation of male reproductive effort influences the size of male secondary sexual characters, specifically male forehead patch size (Gustafsson *et al.* 1995; Ellegren *et al.* 1996; Griffith & Sheldon 2001). Male forehead patch size increased if male effort was experimentally decreased in the previous year, while an experimental increase in effort was associated with a decrease in forehead patch size; similar results have recently been reported for male house sparrows *Passer domesticus* (Griffith 2000). In the largest analysis (Gustafsson *et al.* 1995), an increase in brood size of two nestlings was associated with a change in forehead patch size of approximately 0.3–0.4 s.d. (see also Sheldon & Ellegren (1999)). Comparison of feeding rates of males to experimentally manipulated broods suggests that an increase in brood size of two young leads to an increase in the rate of feeding by *ca.* 65% (figure 2).

A major source of sexual selection on male forehead patch size is via variation in paternity among broods—males with large forehead patches sire a greater proportion of the offspring at the nest at which they feed in natural broods (Sheldon & Ellegren 1999). Standardized selection gradients via this pathway, and that due to variation in female fecundity, average about 0.15, suggesting that the effect of increased effort given to two extra nestlings is equivalent to a decrease in future reproductive success of *ca.* $0.15 \times 0.35 \times 0.45 = 2.4\%$. However, male forehead patch size also affects male success in siring offspring in other nests (Sheldon & Ellegren 1999; Sheldon *et al.* 1999*a*), although there are no estimates of the relative strength of this sexual selection pathway available. Thus, we can probably expect the fitness consequences of increased parental effort via sexual selection in future years to be greater than this estimate, perhaps twice as large.

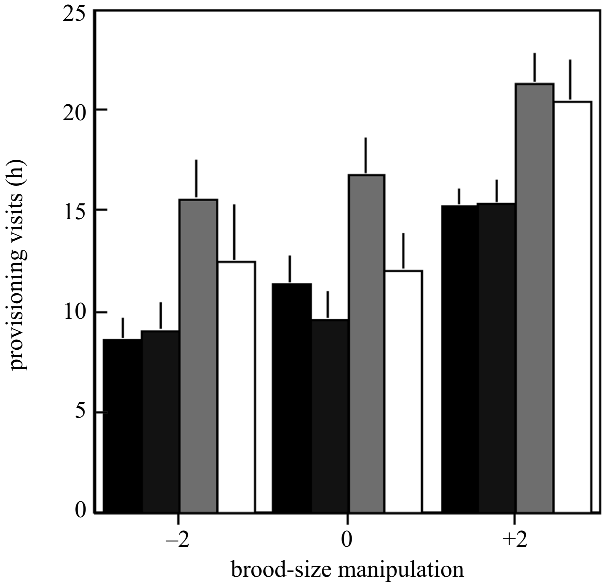

Figure 2. Provisioning rates (mean ± s.e.) of male and female collared flycatchers in response to experimental manipulations of brood size, at two different nestling ages. Black bars, female d6; dark grey bars, male d6; light grey bars, light grey shading, female d11; white bars, male d11.

If a change in male parental care in response to changed certainty of paternity represents an adaptive response, then the change must be associated with a change in the prospects of offspring produced by the current breeding attempt. Whether this is the case can be assessed by determining how variation in paternal care relates to reproductive value of offspring. Controlling for the effects of year, breeding date and brood size on both variables (uncorrected data give similar figures) suggests weak positive effects of the rate of male feeding and the proportion of the feeding visits by the male on the fledging mass of nestlings (table 2). There is no effect of variation in feeding rate of females on the fledging mass of offspring. Fledging mass is generally positively related to recruitment probability in this population (Lindén *et al.* 1992; Merilä *et al.* 2001). Thus, one would expect a relationship between paternal care and recruitment of offspring—this is indeed the case. Male feeding rate, and male share of feeds, were both positively related to the number of offspring fledged from the breeding attempt (table 2).

Hence, at first sight, there is evidence that a male's contribution of parental care to the current breeding attempt is influential in determining its reproductive value. Since we also have evidence that an experimental manipulation which causes a change in male attractiveness also causes a change in male feeding rates (figure 2), it seems reasonable to accept that variation in male parental effort causes a trade-off between current and future reproduction for males. This trade-off is required for there to be selection for males to adjust their parental effort in relation to certainty of paternity.

(d) *Difficulties with the collared flycatcher case*

Although the data described above seem consistent with the suggestion that variation in male parental effort directed at the current breeding attempt will cause variation in the reproductive value of that breeding attempt, and a corresponding change in the opposite direction in the parental male's own future reproductive value, there are several problems with this interpretation. First, although male parental effort seems related to reproductive value of offspring (table 2), these relationships are largely due to pairs in which males provide virtually no care at all. Excluding the pairs where the male's share of provisioning visits is $\leqslant 5\%$, which comprise *ca.* 11% of pairs, the relationship between male parental care and offspring condition and recruitment is not present at all (e.g. in the case of offspring recruitment: male rate of feeding: $F_{1,131} = 1.24$, $p = 0.27$; male share of feeding visits: $F_{1,131} = 0.71$, $p = 0.40$). Thus for most of the range of male parental behaviour we have no evidence that male care makes any difference to this component of offspring fitness. Second, the data relating offspring condition and recruitment to male parental behaviour are not, strictly speaking, experimental. Many of the data were collected as part of experiments which had the effect of causing a response in levels of parental care, but they are not experimental in the sense that a rate of parental care was assigned randomly to different individuals. Since different individuals were thus free to choose their own level of parental care, there exists the possibility that any relationship between male parental care and offspring condition could be caused by another correlated variable (or, equally, that the relationship could be masked by a correlated variable).

A third difficulty is that while data from brood size manipulation experiments suggest that males receiving a decreased brood size enjoy a benefit in terms of increased attractiveness in future years (Gustafsson *et al.* 1995; Ellegren *et al.* 1996), brood-size reduction does not cause a reduction in the rate of nestling feeding by either sex (figure 2). Therefore, it seems unlikely that parental effort measured during the nestling stage captures all variation in parental effort to nestlings. This is worrying, since our main reason for measuring parental effort in a system like this is in the hope that it approximates parental investment. The correlation between the two may in fact be rather poor. Finally, the effects on male secondary sexual character size due to brood enlargement (Gustafsson *et al.* 1995) are relatively large, but implied relatively small fitness differences through sexual selection, because selection on forehead patch size is not particularly strong, and adult survival rates are quite low. However, brood size enlargements were associated with large increases in parental provisioning rate—considerably larger increases than are associated with the experiments seeking to manipulate certainty of paternity (Sheldon *et al.* 1997*b*; Sheldon & Ellegren 1998). The fitness gain from such small reductions in effort would presumably be even smaller. It is possible that these inconsistent results could, in part, be explained by the use of feeding visit rate, independent of the load of food brought, in these analyses. Gathering data on the composition of individual prey loads is much more difficult than simply measuring a rate, but we have no data to indicate whether it is variation in provisioning rate or variation in prey load brought to young that extracts the largest costs from caring parents.

Male collared flycatchers seem to reduce their parental effort in response to certainty of paternity, and there appears, at first sight, to be a plausible mechanism to explain this reduction. However, when one examines the data available for collared flycatchers more closely, it is not clear that this mechanism is very plausible after all. The evidence that a male's share of care to the current brood influences the value of that brood is not strong—any effect of male care seems to be dependent on the male's presence or absence as a parent, rather than on his degree of devotion. Similarly, while changes in levels of care by a male should influence attractiveness in future years, the strength of this effect would appear to be quite weak. In short, both benefits and costs of care seem to be rather small, a situation which Houston (1995) suggested ought to make detection of any response to variable certainty of paternity rather difficult. Thus, while two differing experimental approaches suggest that male collared flycatchers adjust their parental care in relation to certainty of paternity, it is far from clear that we understand why this should be. I discuss more general problems facing empirical tests in § 6.

6. GENERAL DIFFICULTIES

The discussion of work on the collared flycatcher in § 5 suggests that even in well-studied systems it may be very hard to understand whether a relationship between certainty of paternity and paternal investment should be expected. In this section I briefly outline some further problems which make investigation of the relationship between certainty of paternity and paternal investment difficult.

Burley (1986) proposed that individuals might allocate resources to reproduction depending on the characteristics of their mate, for example their mate's attractiveness. This was termed differential allocation. Recent work has shown that differential allocation occurs in many taxa (reviewed in Sheldon (2000)). While differential allocation is one of many factors which can influence a correlation between paternity and paternal care, it could also complicate the interpretation of experimental manipulations. For example, males of different attractiveness might respond differently to the same manipulation of certainty of paternity because the female is prepared to compensate more for an attractive male's reduction in investment than for an unattractive male. Thus, male responses might differ with their attractiveness, and the effect of an experiment on offspring might also differ. This is an example of one of the added complications that biparental care produces for attempting to predict how individuals should behave. As the behaviour of each pair member probably results from a process of 'negotiation' with the other pair member, it may be difficult to predict what the optima for each sex are (Houston 1995).

Recent work using molecular markers to determine hatching sex ratios has shown that avian sex ratios may vary with a range of environmental factors (Sheldon 1998); mate attractiveness is one example of a variable which can influence sex ratios (Sheldon *et al.* 1999*b*). Lessells (1998, 2002) has shown that sex biases in parental care are possible when offspring sexes differ in the relationship between care received and fitness benefit, and that sex differences in parental care are possible when parental functions differ. If both parent and offspring functions differ, interactions between the sex ratio of the brood and the sex of the parents on the amount of parental care received are possible (Lessells 1998, 2002). These effects could greatly complicate effects of experimental manipulations of certainty of paternity if the costs of reductions in care differ between the sexes of offspring.

Finally, complex patterns of mate choice can potentially influence parental behaviour. In the case of the collared flycatcher, Qvarnström *et al.* (2000) showed that the female preference for the forehead patch size of social mates depends on the timing of the breeding attempt. Females show stronger preferences later in the breeding season, and this preference seems to make functional sense since the reproductive success of the breeding attempt depends on the interaction between breeding time and the phenotype of the male. In addition, females seem to adjust their reproductive investment in response to this interaction.

7. CONCLUSIONS

A wide range of models suggest that certainty of paternity can influence male paternal investment. Testing the models is very difficult, but best done using experimental manipulations which influence certainty of paternity. However, there are several problems with interpreting the results of these experiments. One of these is that since certainty of paternity cannot be measured, it is not possible to distinguish between an experiment which fails to manipulate certainty of paternity and an absence of a response to manipulated certainty of paternity (Wright 1998). In addition, the complexity of parental investment likely to occur in most avian breeding systems suggests that there are many possible responses to manipulated certainty of paternity which are not fully considered by the models currently available. Given the difficulty in measuring costs and benefits of parental care in natural systems, it will also be very difficult to decide just what the relationship between certainty of paternity and paternal investment should be. While some experimental evidence supports the existence of facultative responses to variable certainty of paternity, and is hence in agreement with the models, the agreement can only be considered to be very roughly qualitative.

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