Male parental care, differential parental investment by females and sexual selection

ANDERS PAPE MØLLER* & RANDY THORNHILL†

Laboratoire d'Ecologie, Université Pierre et Marie Curie
†*Department of Biology, University of New Mexico*

Abstract. Males play a variable parental role in reproduction, ranging from no male parental care to extensive male care. Females may acquire either direct or indirect fitness benefits from their mate choice, and direct fitness benefits include male parental care. Theoreticians have traditionally emphasized direct fitness benefits to females in species with extensive male parental care. We review the literature and show extensive variation in the patterns of male care, related to the attractiveness of males to females. At one extreme of this continuum, females invest differentially in parental care, investing more when paired with attractive males. The costs of female parental care and other aspects of parental investment may be balanced by benefits in terms of more attractive sons and/or more viable offspring. At the other extreme, in species with extensive direct fitness benefits, males with preferred sexual phenotypes provide the largest relative share of parental care. A comparative study of birds revealed that the extent of the differential female parental investment was directly related to the frequency of extra-pair paternity. Since extra-pair paternity may arise mainly as a consequence of female choice for indirect fitness benefits, this result supports our prediction that differential parental investment is prevalent in species where females benefit indirectly from their mate choice. The consequences for sexual selection theory of these patterns of male care in relation to male attractiveness are emphasized.

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Sexual selection arises as a result of variance in components of mating, or fertilization, success being non-randomly associated with phenotypic traits of individuals of the chosen sex (Darwin 1871). Females are usually the choosy sex, and the fitness benefits accruing to females are either direct or indirect (reviews in Andersson 1994; Møller 1994a). Examples of direct fitness benefits include male resources such as nest sites, territories, nuptial gifts, male parental care and absence of contagious parasites, while indirect fitness benefits include genes for sexual attractiveness and offspring viability.

Organisms in which direct fitness benefits are predominant have traditionally been neglected by

Correspondence: A. P. Møller, Laboratoire d'Ecologie, CNRS URA 258, Université Pierre et Marie Curie, Bât. A, 7ème étage, 7 quai St Barnard, Case 237, F-75252 Paris Cedex 05, France (email: amoller@hall.snv.jussieu.fr). R. Thornhill is at the Department of Biology, University of New Mexico, Albuquerque, NM 87131-1091, U.S.A.

theoreticians because of the intuitive simplicity of the mechanism that could generate a sexual selection advantage (see discussion in Møller 1994a). This is unfortunate because empirical studies have reached divergent results with respect to whether females choosing attractive males obtain more or less direct benefits. Why should females of some species prefer to mate with males that provide much parental care, while females of other species prefer males that provide little care? If parental care is costly, as the empirical evidence suggests (review in Clutton-Brock 1991), then there should be sexual conflict between mates over their relative roles in reproduction (e.g. Davies 1992). This conflict may be resolved to the advantage of females in two ways. If male sexual displays reliably reflect the ability of males to provide extensive parental care, females that choose elaborately ornamented males as mates will obtain a net direct fitness benefit (Andersson 1994; Møller 1994a). Alternatively, individuals of the choosy sex (usually females) may allocate

reproductive effort to offspring sired by the most preferred individuals of the chosen sex as a means of obtaining or maintaining relatively attractive mates (Burley 1986). Females paired with attractive mates may invest disproportionately in reproduction if their offspring thereby increase in quality, and hence the parental investment results in a larger long-term contribution to fitness. Hence, females would obtain an indirect fitness benefit in terms of enhanced attractiveness and/or viability of their offspring. We suggest here that the relationship between the relative role of males in parental care and male attractiveness depends on whether female choice is directed towards direct or indirect fitness benefits.

MALE PARENTAL CARE AND ATTRACTIVENESS

Male parental care is obviously related to sexual selection for direct fitness benefits. Existing models (Heywood 1989; Hoelzer 1989; Grafen 1990; Price et al. 1993) involving biparental care assume that males differing in their sexual displays (e.g. plumage quality or song) directly display their ability to acquire nutrients. For example, males that are adept at finding food items with a high carotenoid content may signal this ability in a slightly brighter phenotype, and if males provide parental care, females mating with such males will rear offspring that acquire food with more carotenoids. Females that prefer to mate with brightly coloured males will therefore initially rear slightly more offspring or offspring of higher phenotypic quality, because the offspring will obtain food with slightly more carotenoids. Brightly coloured males will also experience an advantage because they can acquire females in better body condition and so can start breeding early. Female preference for the most brightly coloured males and male brightness will therefore become exaggerated, even to the extent that male coloration exceeds the optimum under natural selection (Heywood 1989; Hoelzer 1989; Grafen 1990; Price et al. 1993). The prediction of these models is that males with more extravagant displays provide more parental care than less adorned males. Sexual selection due to male sexual displays indicating male parenting ability may be entirely phenotypic, or the male trait may evolve to indicate male genotypic quality and

females may then gain indirect fitness benefits (Heywood 1989; Hoelzer 1989; Grafen 1990; Price et al. 1993).

If males differ in attractiveness, females may, however, have to pay a price for obtaining an attractive mate, for example, by investing differentially in reproduction and males in a free mate market should then prefer to mate with females that invest relatively more in reproduction. Two mechanisms may generate such differential parental investment. (1) The differential access hypothesis proposes that females of high reproductive value have differential (i.e. greater) access to the most attractive males (Burley 1986), and (2) the differential allocation hypothesis proposes that females pay for mating with the most attractive males by investing differentially (i.e. relatively more) in reproduction (Burley 1986). Observational and experimental evidence provides support for both these mechanisms (Burley 1986, 1988; review in Møller 1994a). Since parental care is costly in terms of time or energy (Clutton-Brock 1991), females that invest relatively more in offspring will be at a selective disadvantage unless their investment is balanced by a benefit. The most obvious benefit is that their offspring increase disproportionately in quality, and hence the greater investment results in an enhanced long-term fitness payoff. The sons of attractive males have prospects for high mating success, and the relationship between parental investment and mating success of sons is therefore assumed to be a more steeply increasing function for the sons of attractive males than for sons of less attractive males. Provided that a given level of investment in the sons of highly attractive males increases the number of grandchildren more than does investment in the sons of less attractive males, greater investment by females in the offspring of attractive males will result in a net fitness gain. A similar argument also applies to situations in which males do not provide any care at all, such as lekking species. Females that have managed to acquire a very attractive male should invest differentially (i.e. relatively more) in his offspring, when the benefits from doing so are re-paid in terms of increased mating success of sons.

When should females change from preferring mates that provide a lot of parental care to those that provide little? Intense sexual selection leads to the depletion of additive genetic variance in male secondary sexual character and/or general

viability genes (Fisher 1930; Falconer 1989). However, a directional mate preference may also initially be associated with an increased mutational input that results in a net increase in genetic variance in the male trait and/or general viability (Pomiankowski & Møller 1995). The question of identification of species where indirect fitness benefits are more important is a difficult one. The best candidates are species with signs of past and current sexual selection. For example, the degree of extra-pair paternity, which is unlikely to reflect direct fitness benefits (Birkhead & Møller 1992) is positively associated with the degree of sexual dichromatism in birds (Møller & Birkhead 1994). Further evidence for this hypothesis comes from a comparative study of immune defence and sexual selection in birds indicating that sexually dichromatic species have larger immune defence organs than sexually monochromatic species (Møller et al., in press). Furthermore, bird species with a high frequency of extra-pair paternity are sexually dichromatic and have relatively large spleens for their body size, implying that parasites may play an important role in sexual selection in intensely sexually selected hosts (Møller 1997). Parasites and host immune defences may thus play a general role in sexual selection for indirect fitness benefits in birds and potentially also in other organisms.

Two predictions arise from these theoretical developments. First, if the frequency of extra-pair paternity reliably reflects indirect fitness benefits arising from sexual selection, then male contribution to parental care should be negatively related to the frequency of extra-pair paternity. If male secondary sexual characters reliably reflect attractiveness or viability, males with the most extravagant sexual displays should provide a relatively smaller share of parental care provided by the pair. This prediction rests on the assumption that females engage in extra-pair copulations because they are mated to relatively unattractive males (Møller 1992b). Extra-pair paternity is therefore viewed as an outcome of females adjusting their mate choice as constrained by the availability of attractive males (Møller 1992b). This model is supported by both theoretical and empirical findings (Møller 1992b, 1998).

The second prediction concerns the relationship between differential investment by females in reproduction and male parental care. In the absence of male care, females should invest differentially because of the potential indirect fitness benefits, while benefits may be predicted more often to be either direct or indirect in the presence of male parental care. Hence, there should be a preponderance of differential parental investment on the part of females in the absence of male care, but a mixture of differential and non-differential investment in the presence of male care, depending on whether indirect fitness benefits predominate. This prediction is based on the assumption that increased offspring performance must sometimes be due to relatively greater maternal investment because females are mated to males with superior attractiveness or viability genes.

DIFFERENTIAL PARENTAL INVESTMENT AND EXTRA-PAIR PATERNITY

The first prediction is that males of species with extensive extra-pair paternity should provide a relatively smaller share of male parental care than males of species with little or no extra-pair paternity. We found that in birds with male parental care, attractive males differ considerably in their relative contribution to parental care (Table I). In some species, such as the kestrel, *Falco tinnunculus*, attractive males provide more parental care than less attractive males (Palokangas et al. 1994), while in other species, such as the zebra finch, *Taeniopygia guttata*, attractive males provide less care than less attractive males (Burley 1988). Ten out of 18 species demonstrated a positive relationship between the amount of male parental care relative to that provided by the mate and male sexual displays. Statistically significant positive relationships were found in five species, while statistically significant negative relationships were found in six species.

We assessed the relative role of female choice for differential parental investment from extra-pair paternity. A large difference in extra-pair paternity can be attributed mainly to female choice for indirect fitness benefits (Birkhead & Møller 1992; Møller 1997, 1998). The correlation coefficient relating male care to attractiveness of male plumage characteristics was clearly negatively associated with extra-pair paternity across bird species (Fig. 1a). This relationship remained significant after controlling for similarity among species due to common descent; an analysis of

Table I. Avian studies of sexual selection relating male parental care to the intensity of sexual displays

Species	Character	Statistic	Value	P	r	Plumage score Male	Plumage score Female	Extra-pair paternity (%)	Reference
Falco tinnunculus	Colour*	r_S	0.46	0.03	0.46	4.0	3.0	1.9	Palokangas et al. (1994)
Falco sparverius	Colour§	r_S	0.44	NS	0.44	4.0	3.0	5.0	Wiehn (1997)
Hirundo rustica	Tail length*	r	−0.28	0.001	−0.28	3.5	2.5	28.0	Møller (1992a)
	Tail length*	r	−0.48	0.008	−0.48	3.5	2.5		de Lope & Møller (1993)
	Tail length*	F	102.36	<0.0001	−0.78	3.5	2.5		Møller (1994b)
	Tail asymmetry*	F	51.29	<0.0001	−0.70	3.5	2.5		Møller (1994b)
Parus caeruleus	Breast stripe†	r	−0.39	0.065	−0.39	5.0	5.0	12.7	R. Johnston, unpublished data
Parus major	Breast stripe†	F	0.09	0.77	−0.05	4.5	3.5	14.0	Norris (1990)
Saxicola torquata	Song rate*	r	0.59	0.002	0.59	4.0	1.0		Greig-Smith (1982)
Oenanthe leucura	Stone carrying*	r	0.64	0.019	0.64	2.0	1.0		Moreno et al. (1994)
Luscinia svecica	Colour*	r	0.12	NS	0.12	3.0	2.0	20.5	Reinsborg (1995)
Sylvia atricapilla	Song rate*	r_S	−0.74	0.001	−0.74	2.0	1.5		Hoi-Leitner et al. (1993)
Ficedula hypoleuca	Colour*	t	1.17	0.30	0.14	3.5	2.0	18.5	Lundberg & Alatalo (1992)
Ficedula albicollis	Colour*	t	1.88	0.03	−0.31	3.5	2.5	20.8	Qvarnström (in press)
Passer domesticus	Bib*	r	0.49	0.089	−0.49	2.5	1.0	12.9	R. T. Kimball, unpublished data
Taeniopygia guttata	Colour rings*	g	−0.46	0.004	−0.46	4.0	1.5	28.0	Burley (1998)
Geospiza fortis	Colour‡	r	0.35	0.13	0.35	3.0	1.0		Price (1984)
Carpodacus mexicanus	Colour*	r_S	0.42	0.019	0.42	3.5	1.5	8.4	Hill (1991)
Emberiza citrinella	Colour§	r	−0.65	0.01	−0.65	4.0	1.0	37.4	Sundberg & Larsson (1994)
Dendroica petechia	Colour§	r_S	−0.54	0.001	−0.54	2.0	1.0	37.0	Studd & Robertson (1985)
	Colour§	r_S	0.01	0.96	0.01	2.0	1.0		Lozano & Lemon (1996)
Agelaius phoeniceus	Display*	r_S	0.69	0.0001	0.69	3.5	1.0		Searcy & Yasukawa (1981)

The table reports sexual displays, statistics for the relationship between sexual display and male parental care, plumage brightness scores for males and females and frequency of extra-pair paternity (mainly from Møller & Birkhead 1994).

*Relationship between secondary sexual character and proportion of feeding visits by the pair made by the male.

†Relationship between secondary sexual character and nestling mass.

‡Number of nestlings fed by male.

§Relationship between plumage colour and male feeding rate. Plumage scores were obtained from Møller & Birkhead (1994) and for the additional species not listed there, they were obtained using the same methods by the same scorers.
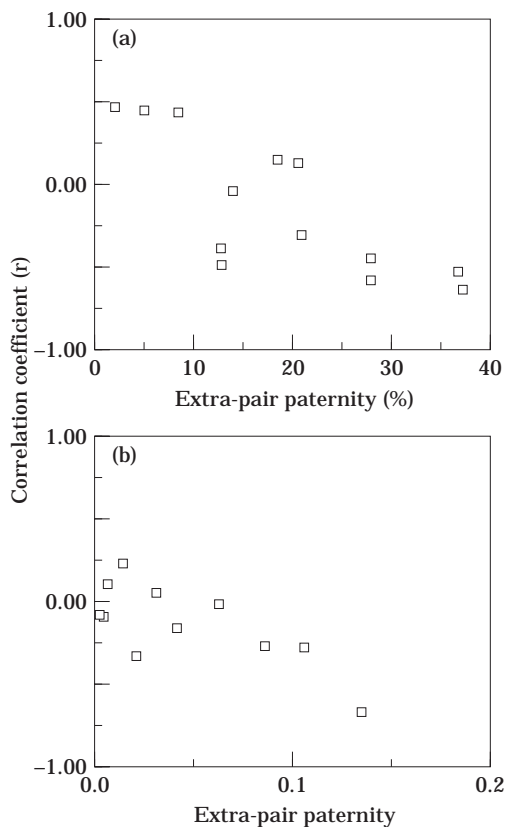
Figure 1. Correlation coefficients relating male care to the attractiveness of male sexual displays in birds in relation to the frequency of extra-pair paternity. The relationship when (a) species are used as observations, and (b) statistically independent contrasts are used as observations, after square root-arcsine transformation of the proportion of extra-pair paternity. Statistics were transformed into correlation coefficients using the methods described in Hedges & Olkin (1985) and Rosenthal (1991), and the data presented in Table I. If more than one study was available for each species, the correlation coefficients were averaged after Z-transformation. Extra-pair paternity data were obtained from the same population as the study of sex roles in male care, whenever possible. Only studies with paternity information based on molecular techniques were used.

contrasts (Purvis & Rambaut 1995) calculated from a phylogeny based on DNA–DNA hybridization (Sibley & Ahlquist 1990) revealed a significantly negative relationship (Fig. 1b; $F_{1,10}=18.39$, $r^2=0.65$, $P=0.0016$, regression coefficient when regression is forced through the origin $b=-3.464$ (SE=0.808)). Extra-pair paternity is positively associated with sexual dichromatism (Møller & Birkhead 1994); however, the relationship between correlation coefficients and extra-pair paternity remained significant when we used a multiple regression analysis with extra-pair paternity and sexual dichromatism as independent variables (model forced through the origin: $F_{2,9}=8.80$, $r^2=0.66$, $P=0.0076$; partial regression coefficient for extra-pair paternity $b=-3.616$ (SE=0.871), $t=4.151$, $P=0.0025$; partial regression coefficient for sexual dichromatism $b=0.059$ (SE=0.097), $t=0.61$, $P=0.56$). Hence, attractive males generally played a less important relative role in parental care when extra-pair paternity was common.

DIFFERENTIAL PARENTAL INVESTMENT AND MALE PARENTAL CARE

The second prediction is that females should more often provide differential parental investment in the absence of male parental care than in its presence. The opportunities for direct fitness benefits are more obvious in species with biparental care or uniparental male care than in species without male care. Table II shows the relationship between female differential investment in reproduction and whether males invest directly in parental care. The species are distributed among the four cells according to information in the primary literature. We have assumed that if a female's reproductive success increases, when mated to an attractive male, this is evidence for differential parental investment, because females should be unable to increase reproductive success without paying a cost for this investment, as in *Harpobittacus nigriceps* and *Aythya valisineria* (Thornhill 1983; Bluhm 1985). Although the classification of species with respect to differential parental investment is based entirely on the relative male contribution to offspring provisioning for the species with male parental care, and on differences in female reproductive success being associated with access to more attractive males for the species without male parental care, we admit that the classification of some species may depend on our interpretations. For example, the results of the studies of *Drosophila melanogaster* by Partridge (1980) and *Vidua macroura* by Andersson (1982) are consistent with models of

Table II. Relationship between male investment in parental care and differential parental investment by females in the offspring of attractive and unattractive males

Differential parental investment by female	Male parental care	
	Yes	No
Yes	*Ophioblennius atlanticus* (Côté & Hunte 1989)	*Diplosoma listerianum* (Bishop et al. 1996)
	Nymphicus hollandicus (Yamamoto et al. 1989)	*Harpobittacus nigriceps* (Thornhill 1983)
	Hirundo rustica	*Hylobattacus apicalis* (Thornhill 1984)
	Parus major	*Gryllus bimaculatus* (Simmons 1987)
	Parus caeruleus	*Gryllodes sigillatus* (Sakaluk 1997)
	Ficedula albicollis	*Polygonus c-album* (Wedell 1996)
	Sylvia atricapilla	*Monochomus scutellatus* (Hughes & Hughes 1985)
	Taeniopygia guttata	*Drosophila melanogaster* (Partridge 1980)
	Dendroica petechia	*Aquarius remigis* (Weigensberg & Fairbairn 1996)
	Emberiza citrinella	*Coturnix coturnix* (Adkins-Regan 1995)
	Passer domesticus	*Pavo cristatus* (Petrie & Williams 1993)
		Aythya valisineria (Bluhm 1985)
		Vidua macroura (Andersson 1982)
No	*Falco tinnunculus*	
	Falco sparverius	
	Saxicola torquata	
	Oenanthe leucura	
	Luscinia svecica	
	Ficedula hypoleuca	
	Geospiza fortis	
	Carpodacus mexicanus	
	Agelaius phoeniceus	

References are given in Table I with the exception of those given directly in this table.

differential parental investment, although other interpretations are mentioned in the published papers. A second example is the negative relationship between male song rate and male parental investment in the blackcap, *Sylvia atricapilla* (Hoi-Leitner et al. 1993). Hoi-Leitner et al. (1995) subsequently showed that males with high song rates also had territories of better quality. Although this may provide evidence for sexual selection in terms of direct fitness benefits, we see no reason why females should provide a larger share of total parental care just because of high territory quality. Hence, we interpret this study as evidence of differential parental investment. The studies are clearly non-randomly distributed: all species without male investment in parental care had females with differential parental investment, while equal numbers of species with male parental care demonstrated differential female parental investment or no differential investment. The second prediction is therefore supported.

IMPLICATIONS FOR SEXUAL SELECTION THEORY

Females of a range of animal species may obtain either more or less parental care from their mates, depending on the latter's relative attractiveness to females. This interspecific variation is related to extra-pair paternity (Fig. 1), indicating that the intensity of female choice is related to the relative role of males in parental care. This pattern of differential parental investment also exists outside birds. For example in humans, a primate with limited sexual dimorphism, attractive men

invest less money and time in their mates than less attractive men (Gangestad & Thornhill 1997). However, men's attractiveness in relation to paternal care has not yet been studied. Since females of a number of species without male parental care also appear to invest relatively more in the offspring of attractive males, the explanation of the phenomenon appears to depend on whether females may obtain indirect fitness benefits from their mate choice. Differential parental investment by females is associated with indirect fitness benefits, while direct benefits accrue to choosy females, when attractive males play a large role in parental care. We openly admit that the data used for this first analysis are of variable quality with some originating from observational studies and others from experiments. The studies also differ with respect to their objectives: some have attempted to test the good parent hypothesis by collecting information on absolute feeding rates, while others have specifically attempted to test the differential allocation hypothesis by measuring relative parental investment. This heterogeneity in studies may obviously cause bias in the data and give rise to problems of interpretation. The effect of such heterogeneity is likely to result in increased noise in the data. Therefore, our results reported in Fig. 1 are likely to be conservative tests of the prediction.

Sexual selection has been suggested to be a continuous process during different stages of the reproductive cycle with components arising from both pre- and post-mating selection (e.g. Thornhill 1983, 1984; Møller 1994a; Eberhard 1996). Cases of females investing in reproduction in relation to the attractiveness of their mates are common in the literature (Thornhill 1983, 1984; Bluhm 1985; Hughes & Hughes 1985; Simmons 1987; Yamamoto et al. 1989; Petrie & Williams 1993). Enforced mating preventing females from gaining access to males of preferred phenotypes reduces components of reproduction such as mating, egg size, egg production and survival of offspring (Bird 1982; Thornhill 1983, 1984; Bluhm 1985; Hughes & Hughes 1985; Simmons 1987; Yamamoto et al. 1989; Cox et al. 1993; Petrie & Williams 1993).

If sexual selection is restricted mainly to pre-mating components (Andersson 1994), this will require more strict interpretations of some of the most famous experiments on sexual selection.

For example, Andersson (1982) manipulated tail length of long-tailed widowbirds, *Vidua macroura*, and recorded the response of females to the experimental treatment by estimating the number of nests on territories before and after manipulation. The increase in the number of nests on the territories of males whose tails were experimentally elongated was interpreted as suggesting that more females were recruited to these territories. However, an alternative interpretation is that the number of females remained constant, but the reproductive investment by females changed in relation to male phenotypes, if females lay more clutches when mated to attractive males. In other words, the results could be a simple consequence of differential parental investment.

A second example concerns the fitness of offspring produced by randomly mated female *Drosophila melanogaster* and by females allowed to choose a mate (Partridge 1980). Offspring produced by the latter females were more viable than offspring produced by forcibly mated females, and this result was interpreted as suggesting that choosy females obtain indirect benefits for their offspring (Partridge 1980). This result was later suggested to arise from only males of superior competitive ability obtaining mates, and since the competitive success of *Drosophila* larvae is directly related to the competitive ability of their fathers, offspring produced by females given a mate choice may have had superior competitive ability (Taylor et al. 1987). Mating and reproductive success have also been associated with an opportunity to perform mate choice in a number of studies of both invertebrates and vertebrates (Bird 1982; Thornhill 1983, 1984; Bluhm 1985; Hughes & Hughes 1985; Simmons 1987; Yamamoto et al. 1989; Cox et al. 1993; Petrie & Williams 1993). An obvious alternative interpretation is that females mated to attractive males invested more in reproduction, whereas forcibly mated females invested less in current reproduction, because the probability of improvement in the quality of mates, and hence in the quality of offspring, was high in future reproductive events.

Differential parental investment may also be used for alternative interpretations of a number of other phenomena related to sexual selection theory. For example, male parental care in terms of provisioning of offspring is negatively related to certainty of paternity as measured by the proportion of offspring that are extra-pair (Møller &

Birkhead 1993). This result was interpreted as suggesting that males reduced their investment in parental care as a result of reduced certainty of paternity. However, if females pursue extra-pair copulations in an attempt to acquire good genes for their offspring or attractiveness genes for their sons, females may provide more parental investment in order to obtain pair bonds with more attractive males. This would result in a negative relationship between overall level of male care and extra-pair paternity.

These considerations obviously have important implications for empirical studies of direct and indirect fitness benefits of sexual selection. Reliable estimates of the magnitude of the importance of so-called good genes will be affected by differential female parental investment. Obviously females will invest more only if they benefit in terms of increased viability or attractiveness of their offspring. Reliable estimates of the magnitude of the effect of good genes or attractiveness genes can be obtained only by means of artificial insemination, because that will prevent females from investing differentially in their offspring. Alternatively, it may be possible to fool females into believing that they are mated to a male of a different phenotype when rearing subsequent broods. If offspring viability or attractiveness of sons remains unchanged in response to this treatment, and is positively associated with the phenotype of the sire, this provides clear experimental evidence for an indirect fitness benefit. Such experiments will obviously demand a high level of ingenuity and skill from the empiricists.

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