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# Should advertising parental care be honest?

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Species with paternal care show less exaggerated sexual ornamentation than those in which males do not care, although direct benefits from paternal care can vastly exceed the indirect benefits of mate choice. Whether condition-dependent handicaps can signal parenting ability is controversial. The good-parent process predicts the evolution of honest signals of parental investment, whereas the differential-allocation model suggests a trade-off between the attractiveness of a mate and his care-provisioning. I show that both alternatives can arise from optimal allocations to advertisement, parental investment and future reproductive value of the male, and that the male's marginal fitness gain from multiple matings determines which option should apply. The marginal gain is diminishing if opportunities for polygyny or extra-pair copulations are limited. Advertisement is then expected to be modest and honest, indicating genetic quality and condition-dependent parental investment simultaneously. Increasing marginal gains are likely to be related to cases where genetic quality has a significant influence on offspring fitness. This alternative leads to differential allocation with stronger advertisement, more frequent extra-pair copulations, and diminished male care. Reliability is also reduced if allocation benefits have thresholds, e.g. if there is a minimum body condition required for survival, or if females use a polygyny-threshold strategy of mate choice.

**Keywords:** parental care; honest signalling; handicap principle; sexual dimorphism; extra-pair copulations

## 1. INTRODUCTION

Sexual advertisement in species where direct benefits are important has evoked less theoretical attention than the problem of the lek paradox in polygynous species (Andersson & Iwasa 1996). However, variation in direct effects, such as territorial resources or parental care, can be considerably higher than the presumably slight genetic benefits (Kirkpatrick & Barton 1997): as an example, consider paternal care in fish where some males cannibalize the whole of their brood (Lindström & Sargent 1997; Okudu *et al.* 1997). Two hypotheses predict different relationships between the attractiveness of males and their parental investment. The good-parent process (Heywood 1989; Hoelzer 1989) suggests that advertisement signals can indicate good parenting ability. In contrast, the differential-allocation model (Burley 1986) assumes that attractive males provide less parental care since their mates are willing to increase their share in order to keep their partners.

Many studies report that sexual signalling corresponds to variation in male parental investment or to the resources available to the male (Trumbo & Eggert 1984; Hill 1991; Knapp & Kovach 1991; Frischknecht 1993; Moreno *et al.* 1994; Palokangas *et al.* 1994; Welling *et al.* 1997; Wiehn 1997; Linville *et al.* 1998; Wilson 1998). Such correlations suggest honesty, in the sense that the female will obtain direct benefits from favouring a stronger advertisement. Other examples, however, exist where attractive or actively courting males provide less care (Burley 1988; de Lope & Møller 1993; Burley *et al.* 1996; Qvarnström 1997; Raouf *et al.* 1997; Griffith *et al.* 1998), a prediction generated by the

model of differential allocation. Yet other studies show no clear correlation between signalling and care (Yasukawa *et al.* 1987; Wright & Cuthill 1992; Sundberg & Larsson 1994; Mountjoy & Lemon 1997), or describe a trade-off between the care-provisioning of the male and other resources he provides (Hoi-Leitner *et al.* 1993).

Patterns of parental care also influence the evolution of sexual ornamentation. It is generally accepted that polygyny is associated with less paternal care and stronger sexual dimorphism (Björklund 1990; Andersson 1994; see also Höglund 1989; Oakes 1992). Comparisons with monogamy and biparental care may be complicated by extra-pair copulations (EPCs). In birds, EPCs interestingly seem to trigger the evolution of different kinds of dimorphisms—structural plumage colours—compared to polygyny with no paternal care, which enhances dimorphism in size and in melanin-based plumage colours (Owens & Hartley 1998). This comparative study of birds confirms the overall tendency that the degree of dimorphism is reduced when sex differences in parental care diminish (Owens & Hartley 1998).

A seemingly easy explanation for modest ornaments would be that it is not in the interest of the female to favour handicaps that impair the male's ability to provide parental care. Consequently, it has been suggested that signals for parental investment should not have costs that reduce parenting ability itself, so as not to destroy the common interest of high fecundity of the breeding pair (Fitzpatrick *et al.* 1995; Berglund *et al.* 1997). However, this stands at odds with the view that only costly signals can be reliable when signallers and receivers have conflicting interests (Grafen 1990*b*), as is the case when

both high- and low-quality males benefit from being accepted as mates, but females benefit from being choosy.

Models addressing this question have hitherto produced conflicting results (Westneat & Sargent 1996). In some models, parental quality can be signalled by a condition-dependent handicap, but this is achieved either by assuming *a priori* that the signal is honest (Hoelzer 1986), or by assuming that the cost of the signal is paid by the male's viability while his fecundity remains unaffected (Heywood 1989; Grafen 1990a; Perrin 1995). Conversely, Kirkpatrick *et al.* (1990) concluded that although some degree of ornamentation can evolve under female choice in monogamous breeding systems, females should favour less conspicuous males when parental care is important. Price *et al.* (1993) modelled a situation where female choice for direct benefits can lead to reduced average fecundity, higher costs (e.g. reduced paternal care) in ornamented males, and, at equilibrium, no correlation between fecundity and the indicator trait of the male. Recently, however, Wolf *et al.* (1997) have presented a model of paternal and maternal effects, with the result that signalling direct benefits can be honest, assuming that care-provisioning is genetically determined and heritable.

In this paper, I generalize the above results to show how the different alternatives of honesty, dishonesty, and the conflict between parental investment and total quality can all emerge from a single model of optimal allocation to mating success, parental care, and self-maintenance of the male. This diversity emerges when the considered range of possible trade-offs is wide enough. The model is applicable whether or not there is a genetic component to a male's phenotypic condition, but the existence and relative importance of genetic viability differences will affect the outcome of the model.

## 2. HONESTY AND THE SHAPE OF TRADE-OFFS

### (a) *Trade-off between advertisement and survival*

In condition-dependent handicap models (e.g. Grafen 1990a,b), honesty is generated when the optimal balance of costs and benefits of signalling implies increasing advertisement effort with increasing phenotypic quality  $Q$ . In the classical setting, the female attempts to choose a male with the highest possible  $Q$ . The optimal allocation will maximize the quantity  $w(A, P, Q)$ , where  $A$  is the allocation put into advertisement by the male, and  $P$  is the perceived value of the male (*sensu* Grafen 1990a). To provide a simple example, I assume that  $w(A, P, Q) = m(A) + r(Q - A)$ . Here,  $m(A)$  gives the gain (expected fitness) through current mating success when a male's allocation to advertising equals  $A$ ; it is an increasing function if  $P$  increases with  $A$ .  $r(S)$  gives the expected future component of the male's fitness gain (i.e. his residual reproductive value) according to allocation  $S = Q - A$  left for his self-maintenance. The gain  $r(S)$  may vary in shape, as it summarizes the combination of future survival and reproduction. However, regardless of the details of how resources are allocated in the future, it is reasonable to assume that it is an increasing function of allocation  $S$  ('body condition') left after the breeding season. In addition,  $m(A)$  will be increasing if females find advertisement attractive. Hence, the viability cost of signalling,  $A$ , is expressed as a decrease

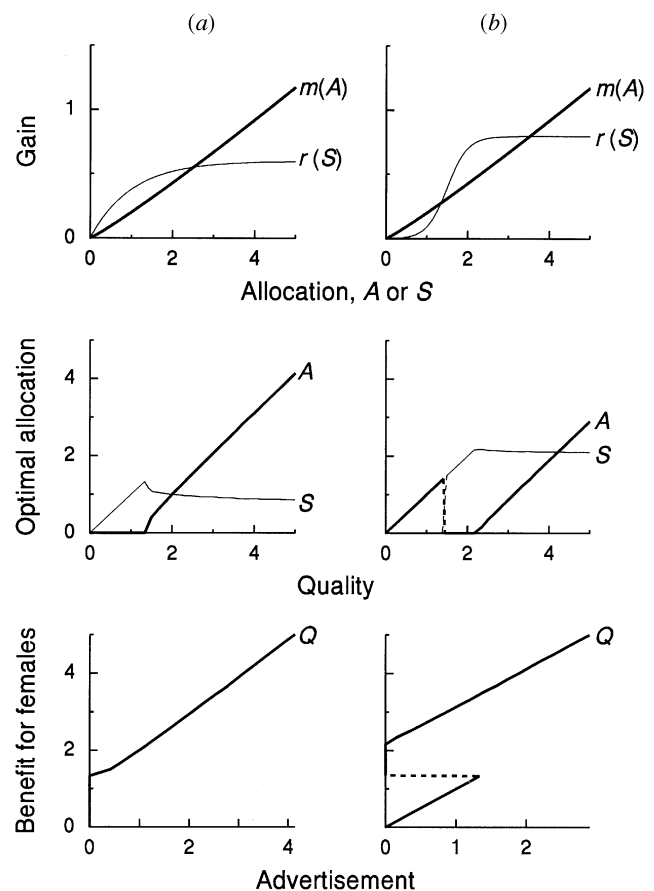


Figure 1. Optimal male allocations into advertisement and self-maintenance with no paternal care, obtained by setting marginal gains equal:  $m'(A) = r'(S)$  (Lloyd 1988). Allocation into mating success,  $A$ , or self-maintenance,  $S$ , can yield varying gain shapes  $m(A)$  and  $r(S)$  (upper row). As a consequence, the optimal allocation into advertisement or self-maintenance may depend nonlinearly on the total quality (middle row). The optimum behaviour is honest if total quality increases with advertisement (lower row). In (a), honesty is fulfilled with all male qualities, although net survival of advertising males decreases with signal intensity. In (b), gain in survival has a concave-convex shape, which results in switches in the optimum strategy as marginal gains are alternately greater and lower for survival than for mating success.

in the future gain  $r(Q - A)$ , while it brings about a benefit through current matings,  $m(A)$ . Signalling is honest if an individual of higher total quality  $Q$  has a larger allocation to advertisement,  $A$ .

Honest signalling in systems with no parental care can thus be exemplified analogously to the general form of a life-history trade-off. Honesty will usually hold in this setting (figure 1a), but sometimes the shape of the trade-off between survival and mating success may cause deviations from strict correspondence between total quality and current advertisement (figure 1b). Advertisement is prone to dishonesty if the future fitness component  $r(S)$  has a concave part, which happens if the gain is characterized by thresholds: there might be a minimum body condition below which survival is virtually impossible, or a certain investment may be required to retain the physiological state required for reproduction. Signal dishonesty is explained by noting that these cases

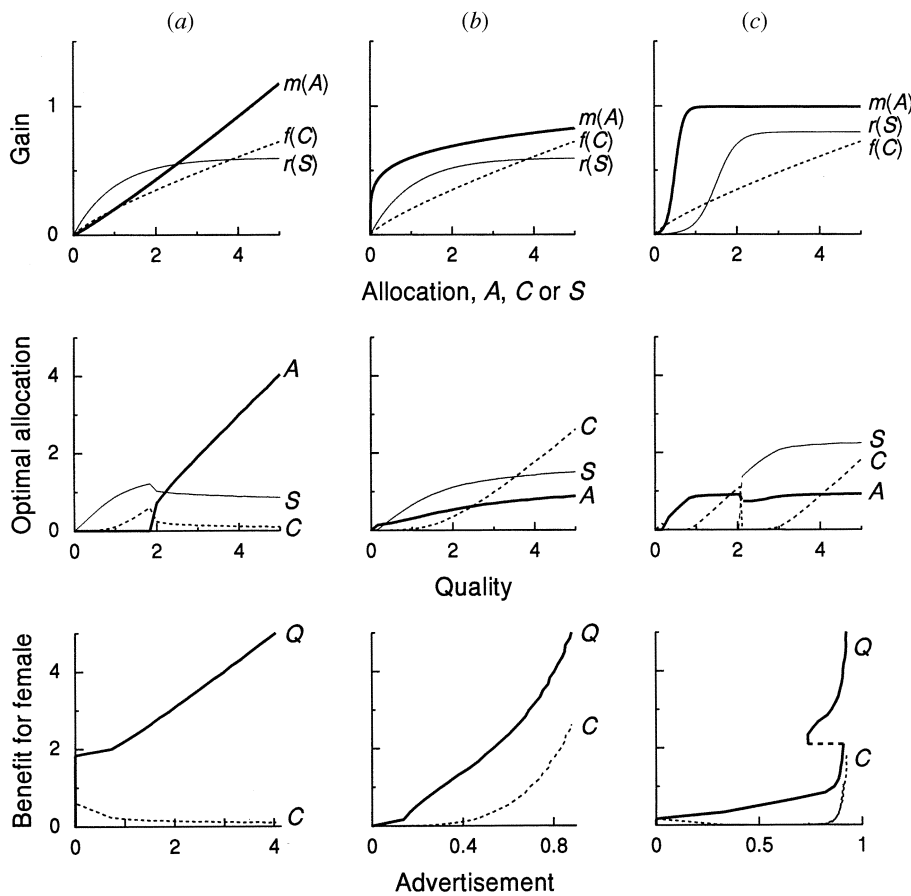


Figure 2. Optimal male allocations into advertisement, self-maintenance and parental care. Investments and gains from parental care are indicated with a dotted line, other explanations as in figure 1. Note that the higher variation in  $Q$  than in  $C$  (lower figures) does not necessarily mean that it is a more important factor for female choice. (a) When gains from advertisement increase faster than from other fitness components, advertisement indicates lower rather than higher parental care, although it is still correlated with total quality. (b) When gains from advertisement have diminishing returns, advertisement signals both total quality and parental care simultaneously. (c) Concave-convex gains of any fitness component can cause abrupt changes in optimum strategies.

do not satisfy the condition that lower quality should impose greater costs when giving a signal (Grafen 1990a). In the example of figure 1b, a low-quality male with already very low survival prospects suffers a smaller reduction in survival if he increases his advertising by one unit than a male with intermediately high survival. Hence, low-quality males advertise as a terminal effort, whereas medium-quality males focus on their survival, and only highest-quality males can allocate effort into both advertisement and survival. As a consequence, a female that encounters a male with advertisement effort 1 has no means of telling whether his true quality is 1 or 2.5, if assessment is based only on  $A$  (figure 1b).

It can be shown that interpreting such deviations in a population-wide context will ensure honesty holds in the average sense: females, on average, still benefit from relying on the signal when the whole age-structured population of males is considered (Kokko 1997, 1998). Hence, honesty can remain valid to a certain extent even if trade-offs do not completely satisfy the condition of differential costs (Grafen 1990a). Such cases do not necessarily require very anomalous trade-offs (Hurd 1997; Kokko 1997; figure 1b).

#### (b) Trade-offs between advertisement, survival and parental care

When it is in the interest of the female to pay much attention to the parenting intentions of the male, and less to the male's total quality, the situation changes (figure 2). The male now has three allocation decisions: advertisement  $A$ , care  $C$ , and self-maintenance  $S$ . I again assume that allocations have an additive effect on fitness gain:

$w = m(A) + f(C) + r(S)$ , where  $A + C + S = Q$ . Thus, mating success as such gives a reproductive gain  $m(A)$  for the male, but this can be increased by  $f(C)$  when providing care for the offspring. Because  $A$  and  $C$  are separate variables, there is the possibility of having a trade-off between the two components of current reproductive success,  $m(A)$  and  $f(C)$ : if increasing  $A$  reduces  $C$ , a more showy male may spend less time feeding the offspring or may increase the nest predation rate. However, total quality differences (variation in  $Q$ ) may override this trade-off: in migrating species, for example, a male in good condition might have arrived early and obtained a good territory where food availability compensates for his reduced foraging time. The matter is further complicated by the need to take the allocations into future benefits,  $S$ , into account. For a female seeking direct benefits, the question of honesty is now not whether a larger total phenotypic quality  $Q$  implies stronger advertisement  $A$ , but whether a larger allocation into care,  $C$ , implies a larger allocation into  $A$ , given that differences in  $Q$  exist.

There is no reason to fix the gain functions  $r(S)$ ,  $m(A)$  and  $f(C)$  to any specific form; e.g.  $f(C)$  may include the compensation provided by the female to varying degrees of care  $C$  provided by the male. Each of the gains should, however, be an increasing function of the corresponding allocation  $S$ ,  $A$  or  $C$ . Specifically, increasing advertisement  $A$  while leaving care-provisioning  $C$  unchanged is assumed to increase the current reproductive success of the male. Here, several mechanisms are possible. High  $A$  may yield mates of higher fecundity, leading to assortative pairing according to quality (e.g. Norris 1990; Møller 1991), or reduce the risk of remaining unmated (e.g. Hill *et al.* 1994).

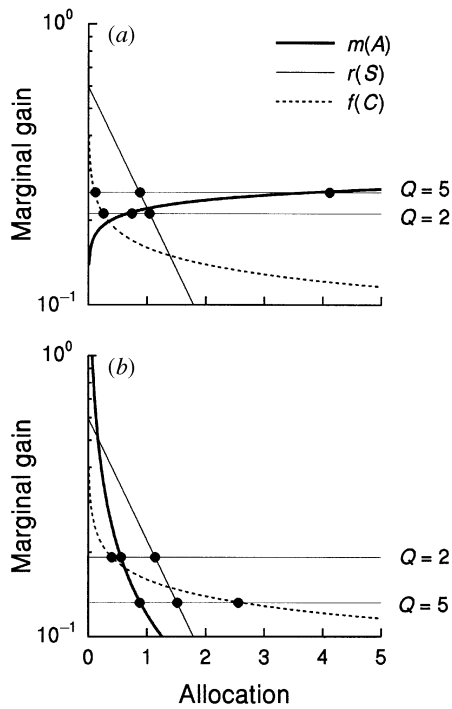


Figure 3. Increasing or decreasing marginal gains of advertisement imply a negative or positive relationship between advertisement and care, respectively. The figure considers solutions where all components receive some allocation, and survival and parental care are both assumed to have diminishing marginal gains. Each condition-dependent optimum must have equal marginal gains and is hence described by a horizontal line. Note that the corresponding total quality  $Q$  is given by the sum of allocations (dots) along the  $x$  axis, not by the height of the line. (a) Increasing marginal gain of advertisement forces higher choices for  $A$  to be linked with lower choices for  $C$  and  $S$ : it is not possible to change the height of the horizontal line without having the change in  $A$  oppose that of  $C$  and  $S$ . Marginal gains are derived from the example of figure 2a (upper optimum,  $Q=5$  ( $C=0.10$ ,  $A=4.04$ ,  $S=0.86$ ); lower optimum,  $Q=2$  ( $C=0.24$ ,  $A=0.73$ ,  $S=1.03$ )). (b) Diminishing marginal gain in both advertisement and other fitness components will lead to higher advertisement always being associated with higher parental investment: a change in the height always brings about either a decrease or an increase in all gain components. Marginal gains are derived from the example of figure 2b (upper optimum,  $Q=2$  ( $C=0.35$ ,  $A=0.54$ ,  $S=1.11$ ); lower optimum,  $Q=5$  ( $C=2.61$ ,  $A=0.88$ ,  $S=1.51$ )).

Alternatively, attractiveness may make the male more successful in becoming polygynous or obtaining EPCs (e.g. Hasselquist *et al.* 1997). High  $A$  may also contribute to a male's fitness if his mate responds by increasing her own parental investment (de Lope & Møller 1993; Swaddle 1996; Wedell 1996), which increases the current reproductive success that the male obtains with a fixed level of care  $C$  (the differential-allocation hypothesis).

In the additive setting, the optimal allocation requires equal marginal gains from each fitness component (Lloyd 1988). It may thus become optimal for a high-quality male to reduce his investment into parental care, if the initial pay-offs from care are relatively high, but the mating gain increases sharply with increasing advertisement effort (figures 2a, 3a). High  $A$  then becomes a signal of low parenting effort, although it remains an honest

signal of total quality  $Q$ . In this case with an increasing marginal gain, two options are possible. If  $Q$  plays little role in female choice compared to  $C$ , females are selected to avoid ornamented males. This breaks down the signalling system, as the initial assumption of increasing  $m(A)$  turns out not to be evolutionarily stable. Signals that advertise parental care and yield increasing marginal gains of mating success for the male should therefore not exist. However, if  $Q$  is sufficiently important for females to make the benefit of mate quality override the cost of obtaining less care, the assumptions of the differential-allocation hypothesis are fulfilled. Thus, whenever  $m(A)$  has an accelerating shape in a stable signalling system, the model predicts a conflict between choosing a male's commitment to care and his genetic quality (or, alternatively, site quality, if  $Q$  indicates good local resources).

By contrast, if mating success  $m(A)$  shows diminishing marginal gains, it is beneficial for the male to spread an increase of his phenotypic quality  $Q$  more evenly into all three components of advertisement, parental investment and self-maintenance (figures 2b and 3b). This will restore the honesty of advertisement, which serves the dual purpose of signalling both parenting ability and genetic quality at the same time (figure 2b, lower row). Advertisement effort, as a whole, remains at a less exaggerated level, and parental investment is increased (figure 2b), especially so if marginal gains of mating success drop faster than those of care-provisioning (figure 3b). The requirement that all marginal gains must become equal at the optimal allocation (Lloyd 1988) guarantees the generality of the conclusion. When marginal gains increase for one fitness component but decrease for others, an increase in other components is always linked with a decrease in the odd one (figure 3a), whereas all allocations must change in the same direction if they all have decreasing gains (figure 3b).

The above analysis assumes that care and self-maintenance both give diminishing marginal gains, generating the negative association between parenting effort and other fitness components when marginal gains of mating success increase (figure 3a). Diminishing gains from care and self-maintenance seem a plausible assumption in most cases, but exceptions might exist, e.g. if survival over the next winter requires a threshold resource level. As in the case of no parental care, anomalous outcomes with abrupt changes in optimal behaviour are possible if any of the gain functions have both concave and convex parts (figure 2c presents an example).

The shape of the advertisement pay-off therefore determines whether females can use advertisement as an honest cue of total quality, parental investment or both. This shape in turn is affected by patterns of female choice, which is easily confirmed by a simple simulation (figure 4). In the simulation, 500 females choose their mates from a population of 500 males. Males differ in condition, which is assumed to lead to varying male advertisement effort; in the example used here,  $A$  is distributed according to  $\mathcal{N}(10,1)$ . Females also differ in their phenotypic condition, which affects the fecundity of the breeding pair. Each female therefore gives the male a pay-off which is distributed according to  $\mathcal{N}(1,0.1^2)$ . Females are assumed to arrive in an orderly manner, highest qualities first, and they invariably favour the

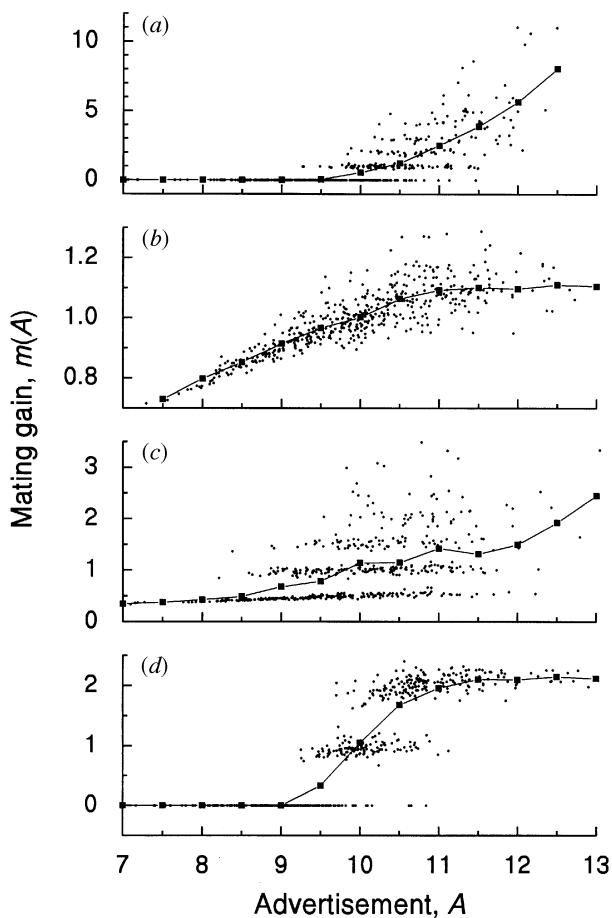


Figure 4. Shapes of mating pay-offs  $m(A)$  generated by a simulation of female-choice patterns with best-of- $n$  choice rule (here,  $n=5$ ). Dots refer to individual males, and squares give the average mating pay-off for males in advertisement categories of width 0.5. (a) Polygyny: when a male can mate repeatedly, expected pay-offs increase sharply with advertisement. (b) Monogamy: when a male becomes unavailable for females as soon as he has mated, pay-offs turn to have a decreasing marginal gain. (c) Social monogamy with extra-pair copulations: each female chooses a social mate as above, but compares his advertisement to two other randomly chosen males, and gives 50% of paternity to the better of these males if his advertisement exceeds that of the social mate. Pay-offs have again increasing marginal gains. (d) Polygyny-threshold choice: females choose best-of- $n$  but prefer to be a secondary female when the advertisement of the already-mated male exceeds that of the solitary male by 0.5 or more. The pay-off is concave-convex as it is determined primarily by the number of females (0, 1 or 2), and secondarily by female qualities.

highest  $A$  found. However, sampling costs restrict them to sample only  $n$  males, i.e. to use a best-of- $n$  choice rule. In addition, depending on whether or not mated males become unavailable for other females, late-arriving females may have to restrict their sampling to the remaining pool of unmated males. EPCs may then also be allowed, giving a fraction of paternity to a freely chosen male, and a fraction to the social mate, the choice of which is more restricted.

As expected, these rules bring about different shapes of  $m(A)$ . Polygyny, where males do not become unavailable through matings, gives rise to a pronounced mating skew, where the few most attractive males fertilize many females (figure 4a);  $m(A)$  is then accelerating, i.e. has

increasing marginal gains. In monogamy, however, variable female quality is the only source of variation in male success, and a male will then not greatly enhance his reproductive success by ever increasing his allocation into attractiveness  $A$ ; the result is a decreasing marginal gain (figure 4b). Moderately expressed but honest signals of parenting ability may then evolve, combined with higher levels of paternal care (figures 2b and 3b). A system approaching polygyny through EPCs (figure 4c) can reverse this pattern and favour increased advertisement in highest-quality males, at the expense of parental care (figures 2a and 3a). Finally, concave-convex shapes may be generated for mating success equally as easily as for survival, for example by assuming that females use a polygyny-threshold strategy that leaves some males unmated but also keeps the fecundity of the best males limited (figure 4d).

Through the relationship between the mating system and the resulting marginal gains, the optimal-allocation model corroborates the view that species with biparental care should have less exaggerated sexual signals. However, it does not require that females select against 'too much' handicapped males (i.e. males with the highest  $A$ ). Females of figure 4b all prefer males with most extreme ornaments, but the mating pattern limits the pay-off function to only be increasing, not marginally increasing. The limitation is due to restricted benefits that a male can gain by increasing his advertisement, despite the existing female preference. A variety of ecological and behavioural mechanisms can contribute to such limitations, such as low population density, synchronous breeding, environmental homogeneity and efficient mate guarding (Westneat *et al.* 1990). Alternatively, gains may become limited if genetic variation is of little interest to females, and they consequently do not seek EPCs: this would restore honest commitment to parental care and allow male ornaments to evolve solely to indicate parental investment.

### 3. DISCUSSION

The logic of the handicap principle is profoundly different in models of indirect and direct benefits. In both cases, the optimum degree by which males reduce their condition by advertisement will vary depending on the shape of trade-offs they face. Specifically, highest-quality males are not always expected to have the highest survival, although they have the highest fitness (Grafen 1990a; Kokko 1998). In good-genes models, this poses no real threat to honesty, as it is the total quality (fitness) that is of interest to the female, not the male's net survival. The problem becomes more severe when the female's interest lies in keeping the male both able and willing to provide parental care. In this case, the female's primary interest is not the total quality from which the male allocates a fraction to advertisement, but his remaining allocation into parenting—which will directly suffer from a handicap.

Thus, although the existence of variation in quality is easier to explain when benefits are direct, restoring the correlation between the expression of the indicator trait and the sought benefit becomes more difficult. The validity of the handicap principle depends mainly on the distinction between diminishing and increasing marginal

gains of advertisement effort, and this is likely to be the main reason why earlier models have produced different outcomes. The 'dishonest' models by Kirkpatrick *et al.* (1990) and Price *et al.* (1993) both use an exponential female-choice function and thus assume increasing marginal gains of the signal. By contrast, Perrin (1995) uses diminishing marginal gains for all fitness components considered, and predicts honest signalling.

The likelihood of observing 'good parents' or 'differential allocations' is linked to the relative importance of direct and indirect benefits as determinants of offspring fitness. The model makes several testable predictions regarding the outcome. The assumptions of the differential-allocation model should be fulfilled if mate sampling is relatively cost-free and offspring success is more dependent on the male's total phenotypic quality than of his direct allocation into care. A sufficiently strong genetic benefit may lead the breeding system towards this alternative end with more frequent EPCs, reduced paternal care, stronger ornamentation, and perhaps ultimately, polygyny with no male care (Petrie & Lipsitch 1994). Plumage dimorphism in birds is indeed linked to the frequency of EPCs (Møller & Birkhead 1994; Owens & Hartley 1998), and the extent of paternal care often correlates negatively with mating opportunities (Westneat *et al.* 1990). As a further refinement, it should be noted that the benefit of mating with a male of high phenotypic quality  $Q$  need not be genetic in order to make the importance of  $Q$  override that of  $C$ , and so produce the outcome of reduced care in high-quality males. Such a case could also occur if a strongly advertising male can attract many females to breed in the same territory, if there is much variation in territory quality, and if losses of paternal care are compensated by higher feeding rates of females mated to a good territory holder.

A firm prediction of the current model is that the shape of the fitness gain from male advertisement should be the key variable that determines the signalling equilibrium. Differential allocations should be linked with a concave-shaped relationship between male mating effort and mating success, whereas the good-parent process requires a convex-shaped relationship. A further prediction—which applies to species with no paternal care as well—is that short-term 'cheats' should be observed if there is a s-shaped (concave-convex) relationship between body condition and future survival, and if male condition is variable enough to make some males fall below the survival threshold. Interestingly, the observation that some starving male sticklebacks increase their brightness (Hosking 1996, cited in Baube 1997) provides a possible example of this alternative. Finally, the model denies the stability of signals that affect male mating success in a concave form and correlate both with the genetic quality of a male and with his parenting effort. Finding such signals would falsify the model, unless it can be simultaneously shown that the fecundity benefit from care also has increasing marginal gains. Developing more detailed models of time-dependence in allocating resources (Westneat & Sargent 1996) may be required if such 'forbidden' cases emerge.

Besides fine-scaled timing, some other aspects of real mating systems are lacking in the simple trade-off model. The model assumes additivity between fitness components, and has therefore less generality than the models of Grafen

(1990*a,b*). Additivity is, however, the most reasonable form of additional fitness benefits such as EPCs (Webster *et al.* 1995), and it also acknowledges the trade-off between current and future reproduction in the correct life-history form. Second, when condition varies in both males and females, mutual mate choice is expected to evolve (Johnstone *et al.* 1996). Positive correlations between female advertisement and her phenotypic quality are found in some species (Møller 1993; Langmore *et al.* 1996), but not in others (Hill 1993; Tella *et al.* 1997), which suggests a possibility of obtaining multiple solutions in systems of mutual mate choice as well. Third, females may maximize care-provisioning not only by choosing a mate, but also by manipulating the number of matings with different males (Harada & Iwasa 1996; Houston *et al.* 1997). This may also be linked with mutual mate choice and lead to female advertisement to maximize mate number (Langmore *et al.* 1996). Further work is required to find the optimum signalling strategies in such systems.

There also remains the possibility that females might be able to observe direct cues of parenting ability instead of handicaps, or use different signals for different qualities. If a female can measure resources directly, without imposing a cost on her mate, she benefits from this reliable assessment while not having to pay the risk that her fecundity is impaired through a lowered care-provisioning ability of her mate. Sometimes, females seem to be able to judge future male care directly, ignoring other traits: sand gobies prefer males of high parenting ability instead of dominant males, although it is unclear how females assess this trait (Forsgren 1997). Commitment to provide care could be signalled through time spent with the female (Langmore & Davies 1997), in which case the cost paid by the male concentrates on his mating success, not parenting ability. Body size has been suggested to be another uncheatable signal, especially in sex-role-reversed species (Berglund *et al.* 1997).

In other words, no handicap is needed to assess either  $Q$  or  $C$ , if  $Q$  is directly observable and optimal  $C$  depends on  $Q$ . As mate assessment and care-provisioning are, necessarily, separated in time, a signal could result from the joint solution of one trade-off between mating success and a future fitness component early in the season, and another between mating success, care and a further future component late in the season, these being linked by total environmental resources  $Q_1$  and  $Q_2$ . Honest advertisement of resources, such as provisioning of nuptial gifts before the time of parental care, may not then require a strict trade-off between advertisement and parental investment to satisfy honesty of resource signalling (Fitzpatrick *et al.* 1995). However, the current model shows that even if the trade-off exists, true handicaps that impair parental ability can evolve to signal parental care, provided that the mating skew remains mild.

Finally, phenotypic quality can give both genetic and direct benefits to the female, which gives the possibility of separate assessment of resources and mate quality. Female pied flycatchers ignore male traits when territories vary in quality (Alatalo *et al.* 1986), but prefer conspicuous males in homogeneous habitats (Lifjeld & Slagsvold 1988). In sedge warblers, both territory quality and song affect the pairing date (Buchanan & Catchpole 1997). EPCs can

further separate genetic benefits from the direct benefits provided by the social mate (Kempnaers *et al.* 1992; Hasselquist *et al.* 1997). EPCs, however, have the potential of not only increasing the variance in male fitness (Webster *et al.* 1995), but also changing the shape of payoffs to destroy the honesty of parental signalling. Direct and indirect benefits from choosing highly ornamented males may coincide (e.g. Møller 1994), but only as long as the gains from increased ornamentation remain limited enough.

After this paper was accepted for publication, the following study appeared, containing support for the prediction that differential allocation strategies are associated with higher frequencies of extra-pair paternity (Møller & Thornhill 1998).

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