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# Will male advertisement be a reliable indicator of paternal care, if offspring survival depends on male care?

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Existing theory predicts that male signalling can be an unreliable indicator of paternal care, but assumes that males with high levels of mating success can have high current reproductive success, without providing any parental care. As a result, this theory does not hold for the many species where offspring survival depends on male parental care. We modelled male allocation of resources between advertisement and care for species with male care where males vary in quality, and the effect of care and advertisement on male fitness is multiplicative rather than additive. Our model predicts that males will allocate proportionally more of their resources to whichever trait (advertisement or paternal care) is more fitness limiting. In contrast to previous theory, we find that male advertisement is always a reliable indicator of paternal care and male phenotypic quality (e.g. males with higher levels of advertisement never allocate less to care than males with lower levels of advertisement). Our model shows that the predicted pattern of male allocation and the reliability of male signalling depend very strongly on whether paternal care is assumed to be necessary for offspring survival and how male care affects offspring survival and male fitness.

**Keywords:** sexual selection; reproductive strategies; male allocation; parental care

## 1. INTRODUCTION

Sexual selection arises as a result of variation in reproductive success owing to inter-sexual mate choice or intra-sexual competition (Darwin 1871). Females are usually predicted to be the choosy sex while males compete to attract mates, either through male–male competition or through the production of a display that signals their attractiveness as a mate, whether through the formation of physical cues such as colourful plumage or elaborate ornaments, or through behavioural cues such as mating dances, nest building, song production or territory defence (Andersson 1994).

In sexual signalling theory, the level of male advertisement (the intensity of colour, the length of an ornament, the complexity of a mating dance) is often argued to evolve as a reliable indicator of a male's quality as a mate; that is the direct or indirect fitness benefits that a female receives for choosing him (Zahavi 1975; Grafen 1990b; Andersson 1994). In species where males provide direct benefits that are important for offspring fitness, such as parental care or nuptial gifts, there should be strong selection on females to choose males that reliably advertise their ability to provide these direct benefits, as choosing the wrong male can have immediate costly effects on female fitness. Theory has suggested that, compared with species without direct benefits, males in species with direct benefits should have more exaggerated display traits, as female preferences for reliable males will select for signals that are costly, difficult to produce or hard to falsify (Grafen 1990b; Price *et al.* 1993). However, empirical work has shown that males in species with parental care typically have less exaggerated sexual

ornamentation than males in species without parental care (Møller & Birkhead 1994; Owens & Hartley 1998).

Both advertisement and parental care are components of a male's reproductive investment and are therefore subject to life history trade-offs in resource investment between fitness-related traits (Stearns 1992; Kokko *et al.* 2002). There are two hypotheses that predict the relationship between investment of resources in male advertisement and parental care. The differential-allocation model assumes that attractive males provide less parental care as their partners will increase their own investment in care to compensate for, and to keep, their attractive mate (Burley 1986). In contrast, the good-parent hypothesis (Hoelzer 1989) suggests that male advertisement may evolve as a reliable indicator of investment in parental care, and defines male care as important for successful rearing of offspring, but not essential. Both of these hypotheses assume that care is biparental and that male care is not required for offspring survival; an assumption that is pervasive in the literature concerning trade-offs between mate attraction and parental care.

The majority of empirical studies examining whether condition-dependent advertisement is a reliable indicator of male parental care have been conducted in birds, a group where biparental care is the most common form of care (Owens & Hartley 1998; Møller 2000; Badyaev & Hill 2002; Duckworth *et al.* 2003). Theoretical models of honest advertisement of care are also often based on biparental systems of care (Price *et al.* 1993; Westneat & Sargent 1996; Kokko 1998; Kokko *et al.* 2002), where females that choose a male that advertises dishonestly are able to compensate for his decreased level of care by increasing their own level of parental care. This focus on biparental and female-only care

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systems has resulted in a gap in our understanding of honest advertisement. In species where male care is necessary for offspring survival, females are unable to compensate for reduction in their reproductive success caused by males that provide less care than advertised. Therefore, selection on females to choose males that reliably advertise the care they provide can be stronger in species with male care than in those with biparental care (Grafen 1990a).

Theory has not examined the reliability of male advertisement of parental care and the allocation of resources between care and advertisement in species where offspring require some male care; although previous work has examined the trade-offs in male investment between advertisement and biparental care. Work in species with male care has focused on the benefits to females of choosing good fathers and the trade-off between offspring care and male survival (Kraak & Weissing 1996; Kraak *et al.* 1999). A recent model of male advertisement of parental care (Kokko 1998) showed that whether a species fits the good-parent hypothesis or the differential-allocation hypothesis depends on a male's marginal gains from multiple matings. This model was intended to apply generally to species where males might provide care, yet allows males to have current reproductive success while providing no care, which makes it inapplicable to species where some male care is required for offspring survival. In this model, male-care provisioning is dependent on the relationship of male mating success to advertisement. If mating success as a result of advertisement is low, as in monogamous species or species with low levels of polygyny or extra-pair copulations, advertisement is predicted to be a reliable indicator of care. If mating success as a result of advertisement is high, as in a polygynous species, males are predicted to put most of their resources into advertisement, and very few or no resources into care. As there are multiple examples, particularly in fish species but also in both bird and insect species, of polygynous species with male-only care (Gross & Sargent 1985; Kraak & Weissing 1996; Ostlund & Ahnesjo 1998; Møller & Cuervo 2000; Tallamy 2000; Hale & St Mary 2007), general theory is needed that examines whether male advertisement is expected to be a reliable indicator of paternal care for species where offspring survival requires some male care.

Here, we extend Kokko's (1998) model to predict male allocation of resources between care and advertisement in species where offspring survival requires some male care. In our model, we ask how a male's allocation of resources to advertisement is affected by the level of care required for offspring survival. We use our model to ask whether male advertisement will be a reliable indicator of male care or quality in species with paternal care. We explore how the relationship between mating success and offspring survival affects the allocation of resources between advertisement and care, and examine its expected effect on female fitness.

## 2. MODEL DESCRIPTION

Our model examines the trade-off in resource allocation between reproductive traits by different-quality males during a single reproductive bout. As with most other models examining the expression of condition-dependent

Table 1. List of variables.

$a$	male allocation of resources to advertisement
$a^*$	optimal allocation of resources to advertisement for males of a given quality
$\alpha_a$	shape parameter for sigmoidal curve $m(a)$
$\alpha_c$	shape parameter for sigmoidal curve $f(a)$
$\beta_a$	shape parameter for power function $m(a)$
$\beta_c$	shape parameter for power function $f(a)$
$c$	male allocation of resources to parental care
$c^*$	optimal allocation of resources to care for males of a given quality
$f(a)$	offspring survival as a result of male investment in advertisement
$f(c)$	offspring survival as a result of male investment in care
$m(a)$	male mating success as a result of his allocation to advertisement
$Q$	male phenotypic quality
$s(x)$	male future reproductive success
$t_a$	inflection point for sigmoidal curve $m(a)$
$t_c$	inflection point for sigmoidal curve $f(a)$
$w$	male fitness
$x$	male allocation of resources to future reproduction

traits (Grafen 1990a,b), we assume that the resources available for allocation to the traits under consideration (male display trait or advertisement,  $a$ , and male care,  $c$ ) are dependent on a male's phenotypic quality,  $Q$ , and that  $Q = a + c + x$ , where  $x$  is a male's allocation of resources to future reproduction (see table 1 for a full list of variables). For simplicity, our model focuses on current investment in reproduction (the trade-off between care and advertisement), and we assume that male allocation between  $a$  and  $c$  has no effect on a male's future survival and reproduction. We therefore define  $Q$  (male quality) as the quantity of energy available for advertisement and care per reproductive bout so that

$$Q = a + c. \quad (2.1)$$

As  $Q$  is the total amount of resources available for investment, increased allocation to one trait is traded off against decreased allocation to another trait. Our model assumes that females choose a mate based on the level of advertisement,  $a$ , that he displays. Male advertisement will be a reliable indicator of paternal care for females when they receive higher levels of male care,  $c$ , for choosing males with higher levels of advertisement (i.e. if an increase in  $a$  is correlated with an increase in  $c$ ) and a reliable indicator of male phenotypic quality,  $Q$ , if  $a$  is positively correlated with  $Q$ . As these models examine the trade-off in resource allocation between traits, it is possible for a signal to reliably indicate male quality while being negatively correlated or uncorrelated with care (Kokko 1998). We ask how the existence of male care within a species affects the reliability of male advertisement as an indicator of paternal care, and how female preference for male advertisement affects the direct benefits they receive in paternal-care species.

Previous theory for paternal-care species assumes that the fitness effects of mating success and offspring survival are additive. In Kokko's (1998) model, males who provide no parental care can still have current reproductive success provided they have non-zero mating success

because male fitness,  $w$ , is the sum of his current reproductive success (his mating success,  $m(a)$  and offspring survival,  $f(c)$ ) and his future reproductive success,  $s(x)$ . As our model considers allocation between advertisement and paternal care within a single reproductive bout, we assume for simplicity that  $s(x)$  is constant and independent of a male's allocation to  $a$  and  $c$ . In this case, Kokko's (1998) fitness equation would be rendered:  $w = m(a) + f(c)$ .

However, a multiplicative equation more accurately reflects the fitness effects expected by most life history models (*sensu* Getty 1998) when male fitness depends on more than one fitness component; e.g. when offspring survival requires some male care. For paternal-care species, male fitness,  $w$ , can be represented by the product of mating success,  $m(a)$ , and the probability of offspring survival,  $f(c)$ , such that

$$w = m(a) \cdot f(c), \quad (2.2)$$

where  $m(a)$  and  $f(c)$  are gain functions. These equations represent the increase in male mating success ( $m(a)$ ) or the probability of offspring survival ( $f(c)$ ) as a function of male allocation of resources to advertisement ( $a$ ) or to care ( $c$ ), respectively. We allow male allocation between advertisement and care within a reproductive event to depend on male quality  $Q$ . Consequently, the predicted patterns of allocation are consistent with male quality being either heritable or environmentally determined. Male quality ( $Q$ ) determines the total resources available for allocation between traits, where males vary in quality between  $0 \leq Q \leq 1$ . The effect of male allocation to care on offspring survival is assumed to be independent of male total mating success (i.e. that allocation to care is shareable). As equation (2.1) implies  $c = Q - a$ ,  $f(c)$  can be rewritten as an expression of  $a$ :  $f(Q - a)$  or  $f(a)$ , allowing us to express  $w$  purely in terms of  $a$ .

We use two different functional forms for  $m(a)$  and  $f(a)$ , which represent different scenarios for how mating success and offspring survival increase with increased allocation to either advertisement or care. We examine four different general cases, by considering all possible combinations of the following functional forms for  $m(a)$  and  $f(a)$ .

(i) *Power function.* The effect of allocation,  $a$ , on male mating success or offspring survival can be represented by power functions such that

$$m(a) = a^{\beta_a} \quad (2.3)$$

and

$$f(a) = (Q - a)^{\beta_c}, \quad (2.4)$$

where for  $\beta < 1$ , the relationship between resource allocation and mating success or offspring survival has a convex shape and shows diminishing returns (figure 1a); if  $\beta = 1$ , resource allocation has a linear payoff (figure 1b); and if  $\beta > 1$ , the effect of resource allocation on mating success or offspring survival has a concave shape and shows accelerating returns (figure 1c).

(ii) *Sigmoid function.* A minimum allocation requirement might exist before individuals obtain high mating

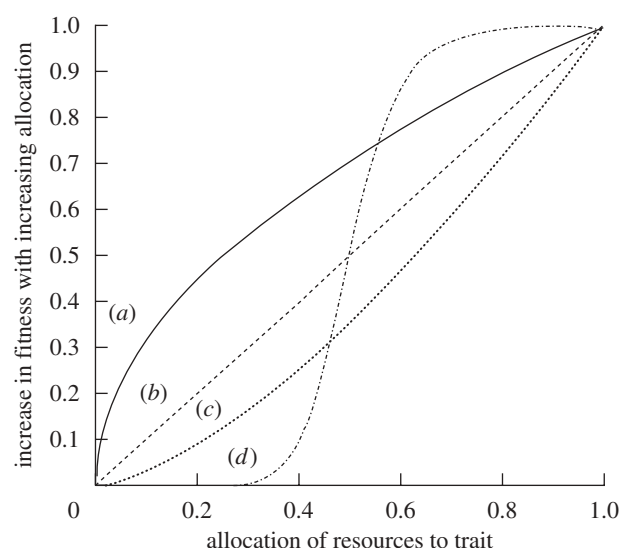


Figure 1. Gain functions for a male's increase in fitness per unit of resources allocated to a trait where allocation (a) has diminishing returns, (b) is linear or (c) has accelerating returns; (d) or gain from allocation has a sigmoidal shape.

success or offspring survival (figure 1d) such that

$$m(a) = \frac{a^{\alpha_a}}{t_a^{\alpha_a} + a^{\alpha_a}} \quad (2.5)$$

and

$$f(a) = \frac{(Q - a)^{\alpha_c}}{t_c^{\alpha_c} + (Q - a)^{\alpha_c}}, \quad (2.6)$$

where  $t$  is the inflection point of a sigmoidal curve where the gain from allocation switches from accelerating returns to diminishing returns;  $\alpha$  is the slope parameter that determines the steepness of the curve: the higher the value of  $\alpha$ , the steeper the curve and the higher the minimum requirement for resource allocation required for high mating success or offspring survival.

To find the optimal allocation of resources between  $a$  and  $c$  for a male of given quality  $Q$ , we differentiate  $w$  with respect to  $a$  to find  $\partial w / \partial a$ , which represents the increase in a male's fitness proportional to his investment in advertisement

$$\frac{\partial w}{\partial a} = \frac{\partial f}{\partial a} \cdot m(a) + \frac{\partial m}{\partial a} \cdot f(a) \quad (2.7)$$

and then solve  $\partial w / \partial a = 0$  for  $a^*$ , which, provided that it represents a global maximum for male fitness, is the optimal allocation of resources to advertisement for males of a given quality,  $Q$ .  $c^*$ , the optimal allocation of resources to care, is found by solving  $c^* = Q - a^*$  (figure 2 shows an example of the trade-off between  $a^*$  and  $c^*$  for males of different qualities).

It can be seen that the assumption that offspring require male care and that male fitness is multiplicative changes the predictions for allocation of resources between advertisement and care when we consider that  $\partial w / \partial a$  for Kokko's (1998) definition of male fitness using our parameters is

$$\frac{\partial w}{\partial a} = \frac{\partial f}{\partial a} + \frac{\partial m}{\partial a}. \quad (2.8)$$

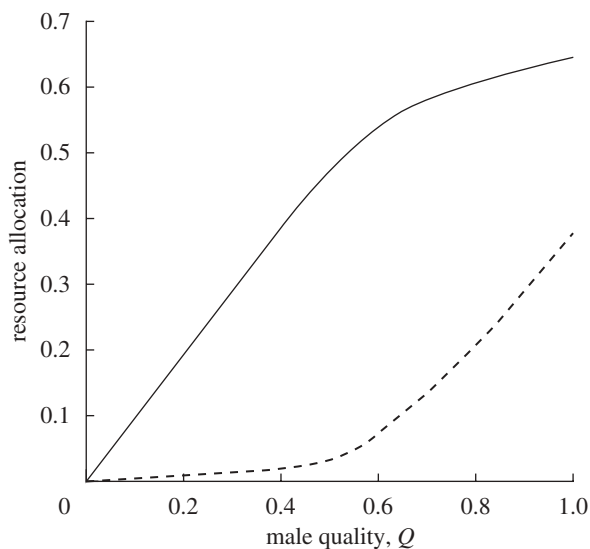


Figure 2. Allocation of resources between advertisement ( $a^*$ ) and parental care ( $c^*$ ) by males of qualities,  $0 \leq Q \leq 1$ , when  $m(a)$  is a power function and  $f(a)$  is sigmoidal,  $\beta_a = 0.5$ ,  $\alpha_c = 10$  and  $t_c = 0.5$ . Males cannot allocate more resources to either trait than they have available to them (their total quality):  $Q^* = a^* + c^*$ . Solid line,  $c^*$ ; dashed line,  $a^*$ .

This shows that the interaction of  $m(a)$  and  $f(a)$  will have less effect on the allocation of resources when male reproductive success is additive (equation (2.8)) than when it is multiplicative (equation (2.7)).

Owing to the interaction between the gain functions and their derivatives in equation (2.7), it is not possible to algebraically solve all of the combinations of our different functional forms of  $f(a)$  and  $m(a)$ . When one of the gain functions has a sigmoidal shape, we must solve  $\partial w / \partial a = 0$  for  $a^*$  numerically using contour plots (in MATHEMATICA).

### 3. RESULTS

Generally, equation (2.7) predicts that whether mating success or offspring survival increases more slowly with resource allocation determines the allocation of resources, as males must maximize their payoff from this limiting gain function to maximize their fitness. In paternal-care species, the presence of male advertisement is an indicator of whether or not a male will provide care. We define advertisement to be a reliable indicator of care if males that advertise more never provide less care than males that advertise less. We define advertisement to be a good indicator of the quantity of care a male provides if increases in allocation to advertisement are closely correlated with increases in allocation to care. In all of the following cases, when  $m(a) = f(a)$ , males allocate their resources equally between care and advertisement.

#### (a) Case 1

When both mating success,  $m(a)$ , and offspring survival,  $f(a)$ , are power functions (as in species where mating success and offspring survival are closely correlated with male nuptial coloration and time spent caring for offspring), male fitness becomes

$$w = a^{\beta_a} (Q - a)^{\beta_c}. \quad (3.1)$$

The direction of selection on male allocation is given by

$$\frac{\partial w}{\partial a} = a^{\beta_a - 1} (Q - a)^{\beta_c} \beta_a - a^{\beta_a} (Q - a)^{\beta_c - 1} \beta_c, \quad (3.2)$$

and it is possible to find the allocation to advertisement ( $a^*$ ) and care ( $c^*$ ) that maximize expected male fitness

$$a^* = \frac{Q\beta_a}{\beta_a + \beta_c} \quad (3.3)$$

and

$$c^* = \frac{Q\beta_c}{\beta_c + \beta_a}. \quad (3.4)$$

These results imply that the trade-off between advertisement and care is driven by the relative value of the shape parameters  $\beta_a$  and  $\beta_c$ . Biologically, a trait with a higher  $\beta$  value must have more resources allocated to it to have the same mating success or offspring survival as the trait with the lower  $\beta$  value (figures 3a and 4a). In this case, male advertisement is a good indicator of both male quality and paternal care (figure 5a), but it will be a better indicator of male care when care is more fitness limiting. This is because when  $\beta_a > \beta_c$ , males allocate more resources to advertisement than to care (figure 3a when  $\beta_a > 1$ ), and advertisement is less closely correlated with care than when  $\beta_c > \beta_a$  (data not shown; increasing  $\beta_a$  results in steeper slopes for care and  $Q$  than figure 5a shows).

#### (b) Case 2

When mating success is a power function and offspring survival is sigmoidal (as might occur in species where mating success is correlated with advertisement but a certain investment in care is required before high offspring survival can be achieved), male expected fitness per reproductive bout ( $w$ ) and the direction of selection on allocation ( $\partial w / \partial a$ ) are given by

$$w = \frac{a^{\beta_a} (Q - a)^{\alpha_c}}{(Q - a)^{\alpha_c} + t_c^{\alpha_c}} \quad (3.5)$$

and

$$\begin{aligned} \frac{\partial w}{\partial a} = & \frac{a^{\beta_a} (Q - a)^{2\alpha_c - 1} \alpha_c}{((Q - a)^{\alpha_c} + t_c^{\alpha_c})^2} - \frac{a^{\beta_a} (Q - a)^{\alpha_c - 1} \alpha_c}{(Q - a)^{\alpha_c} + t_c^{\alpha_c}} \\ & + \frac{a^{\beta_a - 1} (Q - a)^{\alpha_c} \beta_a}{(Q - a)^{\alpha_c} + t_c^{\alpha_c}}. \end{aligned} \quad (3.6)$$

In this case, male advertisement is a reliable indicator of both male quality and care (figure 5b). It is a good indicator of care at lower levels of advertisement. As care is more fitness limiting in this case, males are predicted to allocate few resources to advertisement, and any males that are able to advertise will provide the minimum level of care necessary for offspring survival. In higher quality males that have already surpassed the minimum care requirement, increased advertisement is no longer a good indicator of care but remains a good indicator of quality.

The allocation of resources between care and advertisement is driven by the minimum care requirement for offspring survival. As the minimum allocation requirement increases, males must increase their allocation of

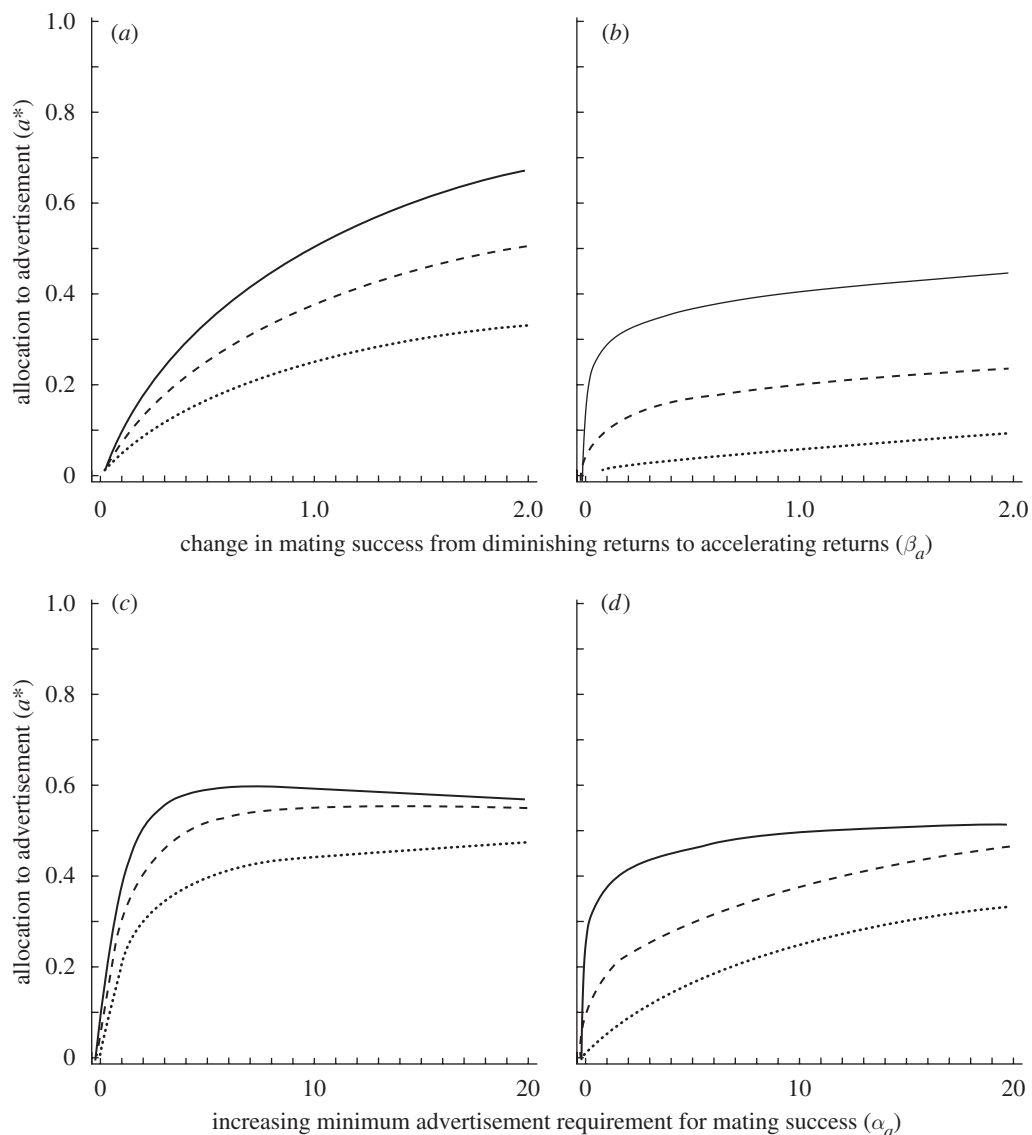


Figure 3. Allocation of resources to advertisement ( $a^*$ ) by males of quality,  $Q = 1$ ;  $Q = 0.75$ ;  $Q = 0.5$  when: (a) both gain functions are power functions and  $\beta_c = 1$ ; (b)  $m(a)$  is a power function and  $f(a)$  is sigmoidal,  $\alpha_c = 10$ ,  $t_c = 0.5$ ; (c)  $m(a)$  is sigmoidal and  $f(a)$  is a power function,  $\beta_c = 1$ ,  $t_a = 0.5$ ; and (d) both gain functions are sigmoidal,  $\alpha_c = 10$ ,  $t_a = 0.5$  and  $t_c = 0.5$ . (a and b) The x-axis shows mating success change from having diminishing returns to having accelerating returns. (c and d) The x-axis shows the minimum advertisement requirement for mating success increasing. Solid line,  $Q = 1$ ; dashed line,  $Q = 0.75$ ; dotted line,  $Q = 0.5$ .

resources to care (figure 4b), as failure to do so will result in zero fitness. However, owing to the shape of the sigmoid function, a higher minimum care requirement for offspring survival will also result in a lower allocation of care required to maximize offspring survival. Higher quality males with enough available resources can maximize offspring survival and invest more in advertisement when offspring survival has a high, rather than a low, minimum allocation requirement.

Once males have invested the required resources in care, the proportion of leftover resources that they invest in advertisement depends on the mating success they acquire in doing so. When a small allocation to advertisement is required for mating success, males invest the majority of their remaining resources in care (figure 3b); as the required allocation to advertisement increases, males will allocate the majority of their remaining resources to advertisement.

### (c) Case 3

When the effect of allocation to advertisement on male mating success is sigmoidal and the effect on offspring survival is a power function (as in species where females are choosy and only mate with males that advertise above a certain level, but the number of offspring that survive is correlated with the amount of care provided), male fitness and the direction of selection on allocation are given by

$$w = \frac{a^{\alpha_a} (Q - a)^{\beta_c}}{a^{\alpha_a} + t_a^{\alpha_a}} \quad (3.7)$$

and

$$\frac{\partial w}{\partial a} = \frac{a^{\alpha_a - 1} (Q - a)^{\beta_c} \alpha_a}{a^{\alpha_a} + t_a^{\alpha_a}} - \frac{a^{\alpha_a} (Q - a)^{\beta_c - 1} \beta_c}{a^{\alpha_a} + t_a^{\alpha_a}} - \frac{a^{2\alpha_a - 1} (Q - a)^{\beta_c} \alpha_a}{(a^{\alpha_a} + t_a^{\alpha_a})^2}. \quad (3.8)$$

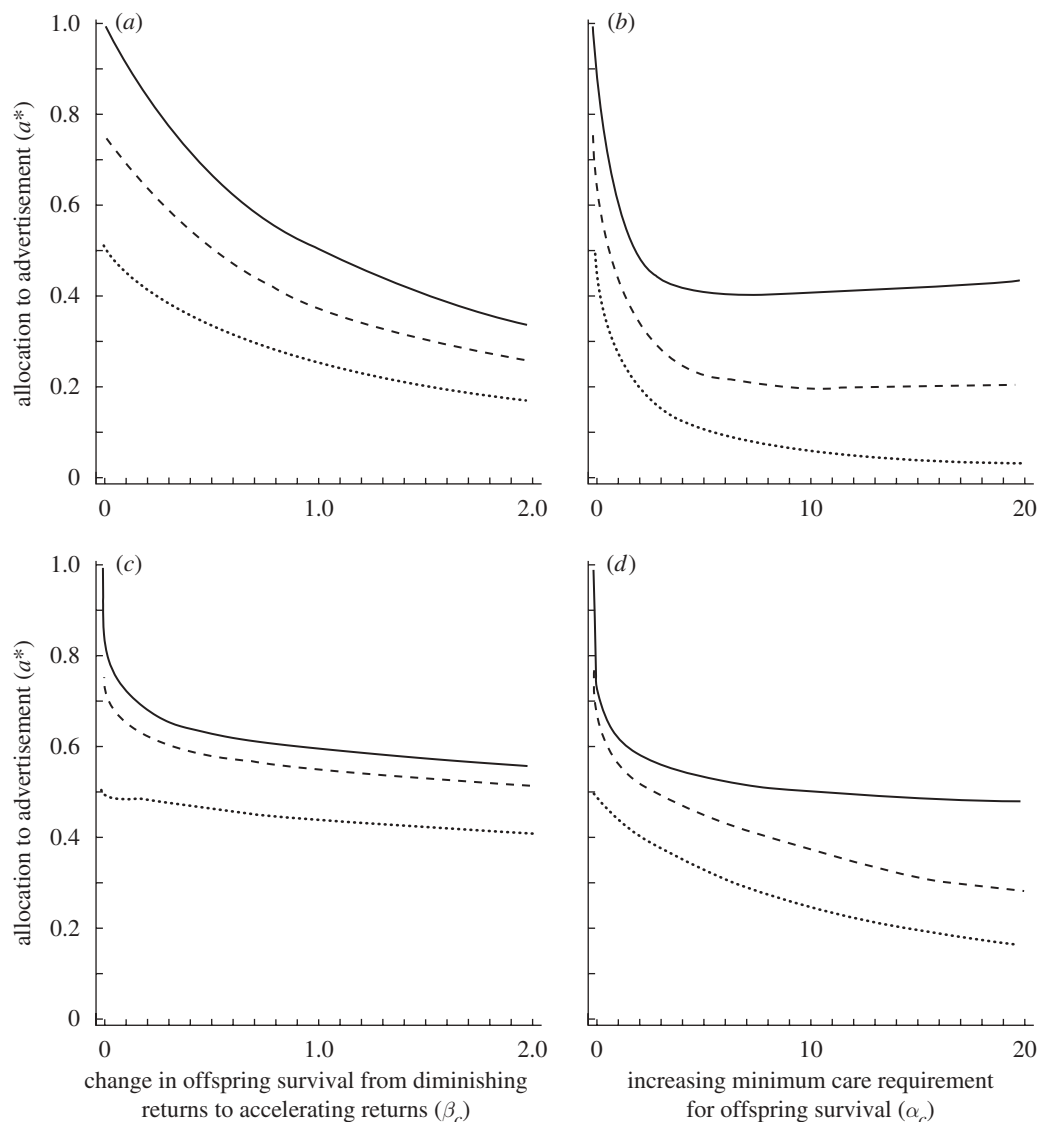


Figure 4. Optimal allocation to advertisement ( $a^*$ ) when  $\beta_c$  and  $\alpha_c$  vary, all other variables and functions are the same as for figure 3: (a) both gain functions are power functions,  $\beta_a = 1$ ; (b)  $m(a)$  is a power function and  $f(a)$  is sigmoidal,  $\beta_a = 1$ ; (c)  $m(a)$  is sigmoidal and  $f(a)$  is a power function,  $\alpha_a = 10$ ; (d) both gain functions are sigmoidal,  $\alpha_a = 10$ ; (a and c) The  $x$ -axis shows offspring survival change from having diminishing returns to having accelerating returns. (b and d) The  $x$ -axis shows the minimum care requirement for offspring survival increasing. Solid line,  $Q = 1$ ; dashed line,  $Q = 0.75$ ; dotted line,  $Q = 0.5$ .

Male advertisement is again a reliable indicator of quality and care. It is only a good indicator of care in high-quality males. Advertisement is not closely correlated with parental care for low- and medium-quality males (figure 5c).

When the minimum advertisement requirement is low, even low-quality males are able to allocate enough resources to have mating success (figure 3c). As the minimum advertisement requirement increases, males must meet this higher minimum allocation requirement, leaving fewer resources to allocate to care; however, owing to the shape of the sigmoidal curve, the allocation required to maximize mating success will also decrease. Higher quality males with enough resources to reach the high minimum allocation requirement are able to subsequently decrease their investment in advertisement and still maximize mating success (figure 3c).

Allocation of any remaining resources to advertisement once the minimum allocation requirement has been

reached is dependent on how much allocation to care is needed for offspring survival. When allocation to care has diminishing returns; males can invest the majority of their remaining resources in advertisement, maximizing mating success. As care allocation begins to show accelerating returns, males allocate less to advertisement and more to care to maximize their fitness (figure 4c).

#### (d) Case 4

When both mating success and offspring survival are represented by sigmoid functions (as in species where females are choosy and offspring require a minimum care investment in order to survive), male fitness and the direction of selection on allocation are given by

$$w = \frac{a^{\alpha_a} (Q - a)^{\alpha_c}}{(a^{\alpha_a} + t_a^{\alpha_a}) ((Q - a)^{\alpha_c} + t_c^{\alpha_c})}, \quad (3.9)$$

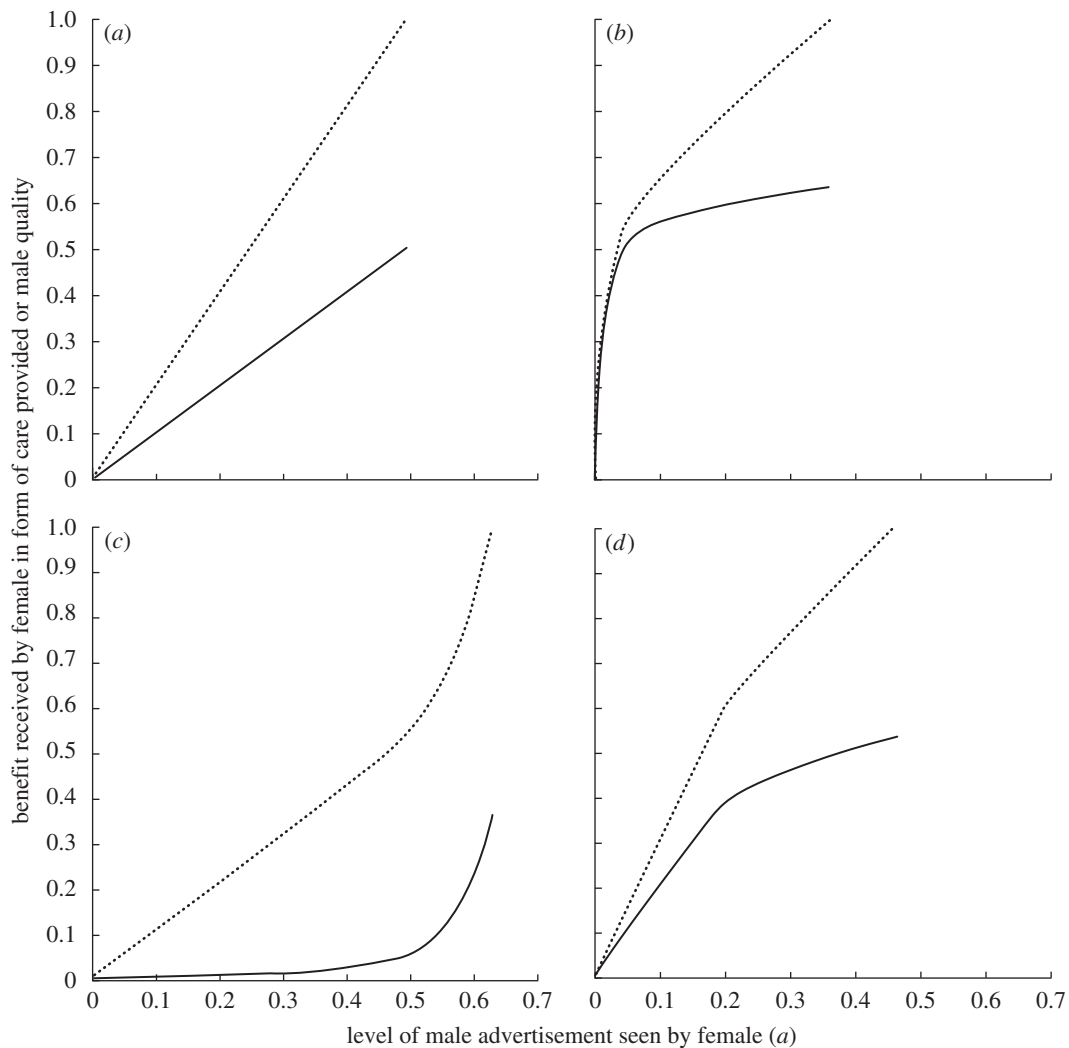


Figure 5. The benefit that a female acquires (male quality or level of resources invested in care) when she chooses a male who advertises at a given level. All functions are the same as for figure 3: (a) both gain functions are power functions,  $\beta_a = 0.5$ ,  $\beta_c = 0.5$ . Male advertisement is correlated with both male quality and parental care; (b)  $m(a)$  is a power function and  $f(a)$  is sigmoidal,  $\beta_a = 0.5$ ,  $\alpha_c = 10$ . Low allocation to advertisement is correlated with high male quality and allocation to care; (c)  $m(a)$  is sigmoidal and  $f(a)$  is a power function,  $\alpha_a = 10$ ,  $\beta_c = 0.5$ . Male advertisement is correlated with male quality but, unless a male has high allocation to advertisement, is not a good indicator of his allocation to care. (d) Both gain functions are sigmoidal,  $\alpha_a = 5$ ,  $\alpha_c = 10$ . Male advertisement is correlated with both male quality and parental care. Dotted line,  $Q$ ; solid line, care.

and

$$\frac{\partial w}{\partial a} = \frac{a^{\alpha_a-1}(Q-a)^{\alpha_c} \alpha_a}{(a^{\alpha_a} + t_a^{\alpha_a})((Q-a)^{\alpha_c} + t_c^{\alpha_c})} - \frac{a^{2\alpha_a-1}(Q-a)^{\alpha_c} \alpha_a}{(a^{\alpha_a} + t_a^{\alpha_a})^2((Q-a)^{\alpha_c} + t_c^{\alpha_c})} + \frac{a^{\alpha_a}(Q-a)^{2\alpha_c-1} \alpha_c}{(a^{\alpha_a} + t_a^{\alpha_a})((Q-a)^{\alpha_c} + t_c^{\alpha_c})^2} - \frac{a^{\alpha_a}(Q-a)^{\alpha_c-1} \alpha_c}{(a^{\alpha_a} + t_a^{\alpha_a})((Q-a)^{\alpha_c} + t_c^{\alpha_c})}. \quad (3.10)$$

In this case, male advertisement is again a reliable indicator of both quality and care (figure 5d). Advertisement is a better indicator of quality and care when allocation to advertisement is lower than when it is higher.

When both mating success and offspring survival have minimum allocation requirements, low-quality males have almost no fitness at all unless both minimum allocation requirements are low (figures 3d and 4d). If either or both minimum allocation requirements increase, low-quality males will not have enough resources available to meet both minimum requirements. In this case, males may not be able to attempt to mate until they reach a

minimum quality level. Medium-quality males will invest the majority of their resources in whichever trait has the higher minimum allocation requirement, as allocating resources to this trait will increase their fitness more than allocating them to the trait with the lower minimum requirement (figure 3d:  $Q = 0.75$ ; compare male allocation to advertisement when  $\alpha_a < 10$  and  $\alpha_a > 10$ ). High-quality males are able to invest proportionally more resources than medium-quality males in traits with a low minimum allocation requirement, where the marginal gains in the trait value for additional allocation above the minimum requirement are low, and proportionally less in traits with a high minimum allocation requirement, where marginal gains are high, thereby maximizing their mating success and offspring survival (figures 3d and 4d).

#### 4. DISCUSSION

In contrast to Kokko (1998) (where reproductive success is additive), our model predicts that male advertisement

will always be a reliable indicator of both male quality and care in paternal-care species. Many of the predictions of Kokko (1998) are reversed in our model. In our model, a slow trait increase is generally associated with a low absolute trait value, which should (and does in Kokko's model) discourage increased investment. However, when the fitness equation is multiplicative, male fitness is more sensitive to changes in the lower of its two factors and a low absolute trait value will encourage investment in that trait, while in Kokko's model, males should invest more in whichever trait has the higher absolute trait value. When mating success has a higher absolute trait value than offspring survival for identical investment levels, Kokko predicts that males should invest more resources in advertisement and provide little care; our model predicts the opposite, that males should invest the greater proportion of their resources in care. Kokko's model predicts no investment in advertisement when offspring survival has a higher absolute trait value than mating success, while the highest levels of male advertisement predicted by our model occur when mating success has a minimum advertisement requirement and, therefore, is fitness limiting (figure 5c). We show that when offspring survival requires male care, advertisement is a reliable indicator of care because allocation is determined by the most fitness-limiting trait, rather than the one whose trait value increases most with increasing investment level.

It is useful to ask how the reliability of male advertisement affects female preferences and the direct benefits from paternal care received by females when we assume that females rely on male advertisement for information when choosing a mate. In some species, male advertisement may be a good indicator of phenotypic quality but not of care (figure 5c). In other cases, only very high-quality males display high levels of advertisement, but lower quality males with much less exaggerated advertisement provide almost identical levels of care (figure 5b).

When offspring survival has a minimum care requirement (cases 2 and 4: figures 3b,d, 4b,d and 5b,d), very low levels of advertisement are correlated with high levels of care and quality, and as advertisement increases, male allocation to care plateaus; increased advertisement becomes an indicator of increased male quality. To maximize the direct benefits from paternal care that they receive, females need not exhibit strong preferences: provided that they have a minimum advertisement requirement for mate acceptance, any male chosen will have maximized his offspring survival. Only high-quality males will exhibit high levels of advertisement, and we assume that high-quality males are rare, as the benefit to females of being choosy decreases with the increasing frequency of high-quality males within a population. If parental care is the most important factor for female choice, the selection pressure in such species is on the minimum level of advertisement for female acceptance of a mate. As low- and medium-quality males have such low levels of advertisement as to be indistinguishable from each other, and the level of advertisement that distinguishes a high- from a medium-quality male is very low, small increases in advertisement translate into large increases in quality. A female's minimum advertisement requirement may be low but result in large increases in

female fitness from both direct and indirect benefits. A species may seem to have low levels of advertisement to empirical observers (Owens & Hartley 1998; Duckworth *et al.* 2003), but may in fact be very competitive; very small differences in advertisement may represent very large differences in male quality.

Conversely, when mating success has a minimum advertisement requirement (case 3), only males that advertise at very high levels provide more than minimal levels of care. Female preference for high-quality, high-advertisement males is built into the model, and this preference will result in high levels of male care and offspring survival (figure 5c); unsurprisingly, as the males that provide care are those who have enough resources to reach that minimum allocation requirement of advertisement. It is surprising that we do not see more empirical evidence of exaggerated male display in paternal-care species (Owens & Hartley 1998; Duckworth *et al.* 2003). It may be that, while a female preference for less exaggerated male advertisement is biologically realistic, high offspring survival with little investment in care will often not be biologically realistic for species with paternal care. A high minimum allocation requirement for mate acceptance may also mean that the costs to females of finding an acceptable mate outweigh the benefits received; lowering the minimum advertisement requirement for mating success lowers the level of advertisement seen in case 3 as a whole, and allows lower quality males to provide more care.

When a minimum care requirement for offspring survival exists (case 2), we make the argument that females should have a minimum advertisement requirement for mate acceptance, a scenario we have already modelled (case 3). However, the correlations between advertisement and care in these two cases are very different: case 2 predicts that, unless male quality is important, females should not choose males with very high advertisement levels; case 3 predicts that females should choose males with very high advertisement levels. The crucial difference between these two predictions is the level of care required for offspring survival. When care is limiting, it is a more important component for male fitness than advertisement; it is only when males can provide minimal levels of care and still have some fitness that we see investment in advertisement become more important than care. Regardless of the case under consideration, females receive the most benefits in both care and mate quality by preferring males that allocate more resources to advertisement.

We have concentrated on exploring situations where mating success is dependent on advertisement and males must care for their own offspring. An interesting extension of our model would be to explore cases where males need not advertise or care for their own offspring, but still have some mating success or offspring survival, such as those where sneaking or cuckoldry occur, by using alternative gain functions for  $m(a)$  and  $f(c)$ .

Our model only examines allocation between advertisement and care within a reproductive bout. If the allocation of energy to future reproduction is included within the model, the reliability of male advertisement as an indicator of male care may no longer be guaranteed. When allocation to future reproduction is fixed, our model applies to iteroparous species. However,

empirical evidence (Candolin 1999; Badyaev & Hill 2002; Badyaev & Duckworth 2003) suggests that when resources for current reproduction must be traded off against those for future reproduction, paternal-care species can dishonestly advertise their ability to provide care. While further investigation is necessary to examine the full range of resource trade-offs that affect male advertisement, our model shows that the predictions of previous theory do not apply to species where male care is necessary for offspring survival and that the expected pattern of male allocation and the reliability of male signalling depend very strongly on whether paternal care is assumed to be necessary for offspring survival.

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