Can too strong female choice deteriorate male ornamentation?

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Competition for limited resources can have fundamental implications for population dynamics. However, the effects of resource depletion have rarely been discussed in the context of sexual selection, even though mate choice typically favours males who outperform others in securing access to some limited resource. Here, we develop a model to investigate the question of resource competition as a form of male–male competition in the context of male sexual displays. We phrase our model in terms of male bowerbirds either searching for or stealing resources (ornamental objects) valued by females, and compare the model findings with published studies of time allocation to various activities in different species of bowerbirds. The basic idea of the model, however, extends to cases where the resource is used less directly for the development of sexual ornamentation, such as males excluding others' access to food. We show that if males compete for resources used in sexual displays, intense female preference for high-quality displays can lead to poorer prospects for efficient choice by females. This is because males benefit from excluding others' access to resources used in displays, damaging the overall efficiency of resource use in the population, and the accuracy with which females can judge male ability to gain such resources. The evolution of female choice may therefore have a self-limiting nature when it poses a selection pressure on male resource acquisition.

Keywords: bowerbird; bower raiding; mate attraction; sexual ornaments; sexual selection; producer–scrounger games

1. INTRODUCTION

Animals regularly find themselves in competition for limited resources, and such contests can have fundamental implications for population dynamics. When competing for a resource that takes effort to locate, animals have two choices: to search for it themselves or to steal the resource from others. For example, in the context of foraging, the decision to steal the resource from others leads to kleptoparasitism, which encompasses a range of behaviours, from the raiding of food hoards through to aggressively gaining access to a food resource (reviewed in Giraldeau & Caraco 2000). The term kleptoparasitism is technically used to refer to interspecific food stealing (Brockmann & Barnard 1979; Ha & Ha 2003), but the range of behaviours applies equally to intraspecific theft.

The question of whether individuals should invest in selfish kleptoparasitism or intraspecific theft versus unselfish searching for a food resource has been considered extensively in producer–scrounger games (e.g. Barnard & Sibly 1981; Vickery *et al.* 1991; Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000). In these games, individuals can either search for food (producers) or search for other individuals that have located food (scroungers) but cannot do both simultaneously (Barnard & Sibly 1981; Vickery *et al.* 1991). An increase in the frequency of scroungers in the population decreases the rate at which food can be discovered, and hence decreases the benefits

that can be gained by an individual (Parker 1984). The benefits gained from the producer–scrounger game are thus frequency dependent, and high levels of interference through scrounging appear, in population terms, to be highly detrimental (see Krause & Ruxton 2002).

While such interference has been extensively studied in the context of foraging, the effects of kleptoparasitism have rarely been discussed in contexts of sexual selection. An interesting example is 'prostitution' in Adelie penguins, where males allow extra-pair females to steal nesting material if they gain extra-pair copulations (Hunter & Davis 1998). Obviously, such exchange of limited resources (in the case of penguins, stones used to build nests) is not beneficial to the overall productivity of the colony. Here, we investigate the broader question of producing versus scrounging in the context of male sexual displays. We shall show that if males compete for resources that are used in such displays, intense female preference for high-quality displays can—paradoxically—lead to poorer prospects for efficient choice. This is because when sexual competition is intense, males benefit from tactics that selfishly elevate their displays at the expense of others. When such behaviour spreads, resources available to generate high-quality displays become diminished.

We phrase our model in terms of male bowerbirds searching for resources (ornamental objects) valued by females. It should be noted, however, that the basic idea of the model extends to cases where the resource is used for ornament development less directly, such as males excluding others' access to food, or to cases where males

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compete to provide females with nuptial gifts. Males of 15 out of the 19 species of bowerbird build more or less elaborate ornamental bowers (Marshall 1954; Cooper & Forshaw 1977; Chaffer 1984; Borgia 1986), which are decorated with coloured items from the surrounding habitat, such as feathers, fruits, flowers, bones, shells and man-made items (Marshall 1954; Cooper & Forshaw 1977; Chaffer 1984; Borgia 1985, 1986; Diamond 1987). Females use bower quality and the number of decorations present on the bower as indicators of male quality, and thus bower quality is an important determinant of mating success in bowerbirds (Borgia 1985, 1995; Borgia & Mueller 1992; Madden 2003; but see Lenz 1994). Bower owners can obtain decorations in two ways, similar to the producing and scrounging methods of foraging: they can search for new items (producer), or raid other males' bowers (scrounger). The fact that males steal decorations has long been known (Marshall (1954) and references therein). The large numbers of decorations present on bowers (e.g. Borgia 1986; Hunter & Dwyer 1997), however, indicates that searching plays a major role in determining the number of decorations on the bower, and therefore the mating success of the bower owner.

The dilemma faced by bowerbirds differs from producer–scrounger games. Not only are the benefits of producing (searching) or scrounging (raiding) frequency dependent, in the sense that the total number of items gathered depends on the behaviour of others (as items can be stolen by competitors), but the benefit gained from those items is also frequency dependent. Unlike scrounging in foraging games, the benefits gained by stealing are both direct and indirect. The direct benefit is an increase in the quality of the stealer's own bower. However, because female bowerbirds select mates on the basis of the quality of the bower and its decorations (Borgia 1985, 1995; Uy *et al.* 2001), a given bower's power to attract females will depend on the quality of the bowers of other males in the area. Clearly, bowerbirds face a double temptation to raid other males' bowers, as raiding not only increases the quality of a males' bower, but it also has the indirect benefit of decreasing the quality of his competitors' bowers, increasing his ability to attract mates and therefore gain offspring. However, if raiding becomes common, then a male needs to spend more time on his bower to protect it from theft. Both raiding and bower defence therefore conflict with time spent searching for new decorations. Additionally, a male must be present on his bower to mate with females, and this also conflicts with the time spent searching for new items, but allows a male to defend the bower against intruders.

If the conflicts between the costs and benefits of raiding and remaining on the bower lead to a decrease in the time available for searching, this poses the question of why the bowerbird mating system does not collapse into selfish raiding and no searching. Here, we develop a game-theory model to determine the evolutionary stable allocation of time to raiding, searching and remaining on the bower, and ask how this allocation influences the quality of the bower as a sexual ornament. Thus, we can investigate the impact of male–male competition for resources, and the influence of female choice on the quality of male sexual ornaments. We can imagine two potential scenarios: bower quality increases with the intensity of female choice

as males strive to produce the best bower, or alternatively, bower quality declines when females become choosier, as males increasingly raid each others' bowers to maximize the difference between their bower and those of their opponents.

2. MODEL

A male bower-owner's strategy consists of the way he divides his available time between three mutually exclusive activities: being in residence at the bower, B , searching the surrounding habitat for new decorations or other materials to improve the quality of his bower, S , and raiding the bowers of other males to steal decorations, R . Being in residence at the bower allows a male to tend and defend the bower and also allows him to observe the surrounding habitat for the presence of male intruders or females. The aim of the current model is to determine the evolutionarily stable proportion of time spent in these three activities (the evolutionarily stable strategy (ESS)), where the strategy used by the population $\{B_p, S_p, R_p\}$ cannot be invaded by a more successful alternative mutant strategy $\{B_m, S_m, R_m\}$. Throughout, we use the subscripts p and m to refer to the population and the mutant, respectively.

Bower quality, Q , ranges from zero to one, where one refers to the highest possible quality bower and zero the lowest. Bower quality increases through three processes. First, bower quality increases through tending the bower (for example, maintaining the bower walls or arranging newly acquired decorations), at a rate proportional to the time spent at the bower, B . Bower quality also increases when the owner searches for and finds new items or successfully raids other individuals' bowers. The rate of acquiring new items by either of these activities is denoted by A .

Total increase in bower quality depends multiplicatively on A and B , as both tending the existing bower decorations and bower structure and searching for new decorations are necessary to maintain quality (for example, newly acquired items will not improve the quality of the bower if the amount spent tending is zero). Furthermore, bower quality cannot increase indefinitely, because of structural constraints. We therefore assume that the best possible bower is indicated by its quality equalling 1, and any increase in bower quality is proportional to the scope for improvement of the bower, $(1 - Q)$. Bower quality therefore improves at a rate $AB(1 - Q)$, which counteracts the natural decay through deterioration over time. This rate of natural deterioration is assumed constant, δ . Additionally, bowers decline in quality when they are raided, and we now proceed to specify these rates.

We assume that raiding is successful only when the owner of the bower being raided is not present on the bower $(1 - B)$. If the owner is present, we assume that he can successfully defend his bower, which makes raiding attempts unsuccessful. We assume that males cannot predict whether a particular bower owner will be present when choosing to visit a bower. For example, bowers may be located such that a given male is unable to view his neighbours' bowers. The benefits gained from raiding are also proportional to the quality of the bowers being raided, Q_p : it is impossible to gain any decorations from bowers

that lack them in the first place. Thus, for the population, the bower quality gain from searching and raiding is

$$A_p = [\alpha S_p + \beta R_p(1 - B_p)Q_p]. \quad (2.1)$$

The loss of quality as a result of other males raiding the focal bower is similarly $-\beta R_p(1 - B_p)Q_p$.

Here, α describes the efficiency of searching as a method of increasing bower quality in relation to tending the bower (that is, the increased amount by which bower quality can increase per unit time spent searching, compared with the potential increase from being present on the bower), and β describes the efficiency of raiding in relation to tending the bower. Thus, for $\beta = 3$, an individual will, all other factors being equal, gain three times as much bower quality through one time unit spent raiding compared with one time unit spent tending the bower. Of course, all other factors may not be equal, such as the quality of the bowers available for raiding (if large, this makes raiding relatively more rewarding); these are included in the equations as specified above.

For the mutant, the benefits of searching and raiding are described by

$$A_m = [\alpha S_m + \beta R_m(1 - B_p)Q_p]. \quad (2.2)$$

We can now proceed to specify the equilibrium conditions for bower quality. For the population, the change in bower quality over time is

$$dQ_p/dt = A_p B_p(1 - Q_p) - [\delta + \beta R_p(1 - B_p)Q_p]. \quad (2.3)$$

Solving for $dQ_p/dt = 0$, we obtain the equilibrium bower quality in the population

$$Q_p = \frac{1}{2\beta(B_p - 1)B_p R_p} \left(\delta + \beta(B_p - 1)^2 R_p + \alpha B_p S_p - \sqrt{D} \right), \quad (2.4)$$

where

$$D = -4\alpha\beta(B_p - 1)B_p^2 R_p S_p + (\delta + \beta(B_p - 1)^2 R_p + \alpha B_p S_p^2). \quad (2.5)$$

For the mutant, changes in bower quality are described analogously to equation (2.3):

$$dQ_m/dt = A_m B_m(1 - Q_m) - [\delta + \beta R_m(1 - B_p)Q_p], \quad (2.6)$$

and the equilibrium bower quality for a mutant in a population using strategy $\{B_m, S_m, R_m\}$ is

$$Q_m = \frac{B_m(\beta(B_p - 1)Q_p R_m - \alpha S_m)}{\delta + \beta(B_m Q_p R_m - B_m B_p Q_p R_m + R_p - B_m R_p) + \alpha B_m S_m}. \quad (2.7)$$

We still need to make assumptions about the benefits of having a bower of specific quality. In bowerbirds, females choose males to mate with following assessment of the quality of several bowers (Uy *et al.* 2000, 2001). Thus, fitness of a bower owner depends on the quality of the bower relative to other bowers in the population. However, species or populations might vary in the choosiness of females. If females are very choosy, they will presumably mate with the owner of the best bower even if the male is not available at the bower much of the time, whereas if mating is random, 'passive attraction' (*sensu* Parker 1983) to males who are available will determine mating success. These effects can be incorporated in a

single equation if we assume the following fitness for the mutant bower owner, W :

$$W = B_m(Q_m/Q_p)^\gamma. \quad (2.8)$$

Here, γ describes how discriminating females are. If γ is high, females pay a great deal of attention to bower quality, mating only with males who have good quality bowers relative to the rest of the population; females are thus extremely choosy. If γ is zero, females pay no attention to bower quality, and mate randomly with any male who is present on his bower.

To find the optimal allocation in three different tasks $\{B, S, R\}$, we perform a numerical search. Beginning with a randomly selected population strategy, we test all mutant strategies where one of the components (B , S or R) is increased or decreased by 1% compared with the population strategy. The resulting strategy is then normalized so that $B + S + R = 1$. The mutant strategy giving the highest fitness becomes the population strategy for the next generation. We iterate for 2000 generations until an ESS is reached. The above procedure yields only one ESS at a time; however, starting from different randomly chosen values for the population strategy, we never found a case of alternative ESSs.

3. RESULTS

We investigate the effect of varying the efficiency of searching (α) and raiding (β), the natural rate of deterioration of bowers (δ) and the degree to which females discriminate between bowers of different qualities (γ). This allows us to ask, for example, how much time males should devote to searching and raiding as opposed to remaining on the bower, waiting for females and carrying out bower maintenance activities, when raiding can be an ESS, and whether males should ever abandon the creation of bowers. We can also investigate how the quality of bowers can vary with these parameters.

First, as the efficiency of searching for new items, α , increases, the ESS time spent searching for new items decreases slightly, whereas bower quality increases (figure 1*a*). This increase is more pronounced when bowers deteriorate more quickly ($\delta = 0.5$, figure 1*b*). As the time spent searching decreases, there is a corresponding increase in the time spent on or near the bower. Unsurprisingly, increasing the efficiency of raiding (β) leads to an increase in the time invested in raiding, and a corresponding decrease in the time spent searching (figure 2). Raiding, however, is not beneficial to bower quality in the population. As raiding increases in efficiency and therefore frequency, bower quality declines. At high values of raiding efficiency, bowers are of extremely low quality.

In many cases (figure 1) raiding is absent from the population. For raiding to occur, it needs to be a much more efficient way to obtain ornate objects than searching, but even when raiding efficiency greatly exceeds that of searching (figure 2), it still occurs very infrequently. Males spend less than 6% of their time raiding even when it is 100 times more effective as a method of improving bower quality than searching and tending the bower (figure 2, $\alpha = 1$). Potential explanations for the scarcity of raiding are considered in § 4.

Figure 1. The effects of increasing the efficiency of searching (α) on the ESS probabilities of a male remaining on his own bower (B , dashed line), searching (S , dotted line) and raiding (R , dot-dash line), and the ESS quality of bowers in the population (Q , solid line), for two rates of bower deterioration (δ): (a) $\delta = 0.1$; and (b) $\delta = 0.5$. Other parameter values used: $\beta = 1$, $\gamma = 1$.

When bowers naturally deteriorate more rapidly, males spend increased time searching for new decorations. Raiding, however, does not become more common in the population with increasing deterioration. Instead, males in a population without raiding (figure 3a) invest more time in searching in this case. Males in a population where raiding occurs (figure 3b) maintain approximately the same level of raiding regardless of the rate of deterioration; again, searching increases. Thus, male behaviour can compensate for changes in the external environment. As deterioration increases further, bower quality decreases (figure 3a), as the decline in bower quality through deterioration is not offset by the increased time spent searching. When raiding occurs in the population (figure 3b), bower quality is low regardless of the rate of deterioration. These results also indicate that male behaviour (searching versus raiding) is a more important determinant of bower quality than the external rate of

Figure 2. The effects of increasing the efficiency of raiding (β) the bowers of other males on the ESS probabilities of a male remaining on his own bower (B , dashed line), searching (S , dotted line) and raiding (R , dot-dash line), and the ESS quality of bowers in the population (Q , solid line). Other parameters used: $\alpha = 1$, $\gamma = 1$, $\delta = 0.1$.

deterioration, and highlights the importance of studying male–male interactions.

Finally, and most interestingly, we investigated the effect of female discrimination on male time investment and bower qualities. When females mate indiscriminately with whichever male is present on his bower (figure 4), males should spend all their time waiting at the bower and no time searching or raiding. In this case, bower quality is zero and males should abandon bower building altogether. As females become increasingly discriminatory, males spend more time searching for new items and less time waiting on the bower. Bower quality rises sharply even with low levels of female discrimination, and then declines, as females become even more discriminating (figure 4). This is an important and counterintuitive result: increasing female discrimination can lead to a decline in bower quality.

4. DISCUSSION

Two main results emerge: first, our model makes a number of predictions regarding time allocation in bowerbirds, and we compare these predictions with published results from a number of bowerbird species. Second, we discuss the predictions regarding the impact of female choice on male–male competition, and the potential effect of this competition on male ornamentation.

(a) *Theft and bowerbird time budgets*

Our model predicts that breeding males should spend a large proportion of their time at the bower (*ca.* 70% or more, figures 1–3). However, observations of bowerbird populations indicate substantial variation in the time spent at the bower, ranging from 3% to 73% (table 1). Our prediction is high because of our assumption that males must be present at the bower to protect their bower from raids and to find females (we assumed that females ignore bowers with no male present). Deviations from these

Figure 3. The effects of increasing the rate of natural bower deterioration (δ) on the ESS probabilities of a male remaining on his own bower (B , dashed line), searching (S , dotted line) and raiding (R , dot-dash line), and the ESS quality of bowers in the population (Q , solid line), for two different raiding efficiencies (β): (a) $\beta = 10$; and (b) $\beta = 50$. Other parameters used: $\alpha = 1$, $\gamma = 1$.

assumptions may explain some of the discrepancy. The time spent at the bower may relate to the risk of being raided, as it does in our model: when raiding is more common, bower residence is predicted to be higher (figure 2). Although a 'common occurrence' (Lenz 1994; Pruett-Jones & Pruett-Jones 1994), raiding does not occur frequently in bowerbirds; studies suggest that a given bower is raided once every 4 days or less (Borgia & Gore 1986; Borgia & Mueller 1992; Lenz 1994; see table 1), or males spend only a small proportion of time engaged in raiding activities (Frith & Frith 1994).

The assumption regarding female behaviour may explain the remaining discrepancies. Out of the three species with comparable measures of raiding, regent bowerbirds *Sericulus chrysocephalus* suffer the highest rate of theft, yet spend the least amount of time on the bower (table 1). However, this species differs from others in that courtship begins in the forest canopy rather than on the bower (Lenz 1994), and so the assumptions of our model are not applicable here. Spotted bowerbirds spend less

Figure 4. The effects of increasing discrimination by females (γ) on the ESS probabilities of a male remaining on his own bower (B , dashed line), searching (S , dotted line) and raiding (R , dot-dash line), and the ESS quality of bowers in the population (Q , solid line). Other parameters used: $\alpha = 1$, $\beta = 10$, $\delta = 0.1$.

time on the bower than satin bowerbirds, yet suffer a lower rate of theft (table 1), suggesting that satin bowerbirds spend increased time on the bower to counteract the risk of raiding. However, to fully test this hypothesis, studies investigating both the risk of being raided and the time spent on the bower, both within and between species, are needed. Our model is not restricted to bowerbirds: penduline tits (*Remiz pendulinus*) face a similar time allocation problem. Males build nests to attract females, and theft of nesting material is more efficient than searching for it, reducing the time taken to build a nest. In this species, males spend up to 80% of their time near their nest, although much less time is needed for construction (Schleicher *et al.* 1993).

In our model, the damage caused by raiding is equal to the benefits gained by the raider, and at equilibrium, all males raid and are raided equally often. Such reciprocal raiding has been noted in bowerbirds (Borgia & Gore 1986; Frith *et al.* 1994). Raiding is often combined with bower marauding, where intruding males partly destroy an opponent's bower in addition to stealing decorations (Pruett-Jones & Pruett-Jones 1994). Thus, the impact of raiding on the victim may exceed the direct benefits gained by the raider (decorations gained), suggesting that the intensity of raiding may be important. Modelling suggests that raiding may only be evolutionarily stable when combined with marauding (Pruett-Jones & Pruett-Jones 1994). At well-decorated bowers, however, males focus on stealing rather than marauding (Borgia & Gore 1986; Borgia 1995); thus, bower quality can impact on stealing behaviour (Madden 2002).

(b) General lessons: male-male competition for resources and sexual selection

A common feature of all sexual selection models so far is that female preferences cause the evolution, and sometimes exaggeration, of male traits (e.g. Lande 1981; Iwasa & Pomiankowski 1991; Pomiankowski *et al.* 1991;

Table 1. Presence on the bower for a range of bowerbird species.

species	mean percentage of time at or near bower (range)	definition of 'near bower' where specified	occurrence of theft	source
satin <i>Ptilonorhynchus violaceus</i>	73	50 m	0.11 thefts per bower per day	Donaghey (1981); Borgia & Gore (1986)
tooth-billed <i>Ailuroedus destirostris</i>	64 (52–79)	'attending court'	0.18% of time	Frith & Frith (1994); Frith <i>et al.</i> (1994)
MacGregor's <i>Ambylornis macgregoriae</i>	54 (20–75)	20 m	no raiding occurs, but spend 2% of time interacting with intruders	Pruett-Jones & Pruett-Jones (1982, 1985)
great <i>Chlamydera nuchalis</i>	47.2			Veselovsky (1978)
spotted <i>Chlamydera maculata</i>	9.6 (8.8–10.4)	'at bower'	0.048 thefts per bower per day	Borgia & Mueller (1992); Madden (2002)
regent <i>Sericulus chrysocephalus</i>	3		0.264 thefts per bower per day	Lenz (1994)

Kokko *et al.* 2002). To our knowledge, it has not been realized before that the effects of competition between males to attract mates can drive selection in the opposite direction. Our model suggests that intensely expressed preferences of females can cause the deterioration of male ornamentation through male–male competition (figure 4). In the context of the bowerbird mating system, this happens if raiding becomes more frequent as females become increasingly choosy. In a wider context, such an effect could occur whenever contests between males to acquire resources necessary for sexual displays lead to deterioration of this resource, in other words a reduced ability to invest in sexual ornaments forming the basis of female choice.

Further work is required to explore the consequences of this mechanism for the evolution of female choice. Could the diminishing male display also mean less accurate female choice, which would probably hamper the further evolution of female choice? This requires us to assess how accurately females distinguish between bowers of varying quality. In our model, at equilibrium, all bowers are of equal quality. However, in natural populations, variation will exist around any trait under consideration (Pomiankowski & Møller 1995). If we expect traits to vary around an equilibrium, the accuracy of female choice will depend on mean trait size as well as the variation available for assessment. Our results have established the self-limiting nature of female choice, whenever choice is easier when the mean male trait is larger. In other words, if strongly choosy females cause such intense male–male competition that traits evolve to be smaller, and if trait size is easier to assess when it is large, then choosiness leads to diminished prospects for accurate choice, and the benefits of being choosy become limited.

Under what conditions would we expect choice to be easier when traits are large or well developed? When a trait is on average large, it may be possible to have a larger variance around it, and thus discrimination may be easier for females. Whether this phenomenon occurs is a matter of empirical research rather than modelling, and thus we have not included it in our study; instead, we discuss here the prospects of finding such a mechanism in nature.

Sexually selected traits are often described as 'elaborate', suggesting that in general, they appear larger or more ornate when compared with other traits that do not form the basis of sexual selection. Darwin (1871) noted that sexually selected characteristics are highly variable, and suggested that this was to allow discrimination by potential mates. Recent meta-analyses (Alatalo *et al.* 1988; Cuervo & Møller 1999, 2001) have found a larger coefficient of variation in sexually selected traits than in ordinary morphological, naturally selected traits. A greater variance suggests that female choice for better quality males should be easier. However, there are few data at present regarding the accuracy of female assessment relative to the degree of trait exaggeration. We simply note here that it is plausible that larger traits have absolutely larger variances. It appears that there are limited data on animals' ability to discriminate between traits of various sizes. Cognitive limitations have mainly been discussed in the context of detecting small degrees of asymmetries in sexual traits (Swaddle 1999a,b). In that context, animals appear to be unable to detect too small (within-individual) differences in the sizes of morphological traits. It is conceivable that a similar cognitive constraint operates when attempting to detect differences between different males; further work is needed in this area. Generally, signals are easier to detect with increasing difference between the signal and the background (e.g. Bushnell *et al.* 2003), but a minimum change in a signal is necessary before the change can be detected (Weber's law (e.g. Shettleworth 1998)).

Whether choice really becomes self-limiting depends on how the mean and variance of male traits respond to male–male competition. Our model suggests that male–male competition may hamper female choice. Alternatively, male–male competition may increase the variance in male sexual ornaments as a result of inequalities in resource use, or the abilities of lower-quality males to tolerate the stress of competition. Such a pattern has been found in sticklebacks (*Gasterosteus aculeatus*), where competition between males enhances variation in coloration used in female choice (Bakker 1994; Rowland 1994). Future models could incorporate variation in male quality (in terms of his ability to construct a high-quality bower)

and stochasticity in the males' decision-making processes and success in developing an ornament and/or attracting females (McNamara *et al.* 1997).

Thus, while we have shown that there is a possibility for self-limiting evolution of female choice via deteriorating resource use efficiency under intense male–male competition, the details of the system may matter. Nevertheless, we have shown that too intense male–male competition can, at least under certain circumstances, lead to smaller ornaments and thus deteriorating accuracy of female choice. This could provide a natural stopping point for runaway evolution of male traits, something that opened models of runaway sexual selection require to be realistic (Kokko *et al.* 2003). To discover if such self-limitation occurs in nature, resource use and interference of males should be studied at different intensities of female choice, and we hope that our study encourages empiricists to do so.

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REFERENCES

- Alatalo, R. V., Hoglund, J. & Lundberg, A. 1988 Patterns of variation in tail ornament size in birds. *Biol. J. Linn. Soc.* **34**, 363–374.
- Bakker, T. C. M. 1994 Evolution of aggressive behaviour in the threespine stickleback. In *The evolutionary biology of the threespine stickleback* (ed. M. A. Bell & S. A. Foster), pp. 345–380. Oxford University Press.
- Barnard, C. J. & Sibly, R. M. 1981 Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–555.
- Borgia, G. 1985 Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* **33**, 266–271.
- Borgia, G. 1986 Sexual selection in bowerbirds. *Sci. Am.* **254**, 70–79.
- Borgia, G. 1995 Why do bowerbirds build bowers? *Am. Sci.* **83**, 542–547.
- Borgia, G. & Gore, M. A. 1986 Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Anim. Behav.* **34**, 727–738.
- Borgia, G. & Mueller, U. 1992 Bower destruction, decoration stealing and female choice in the spotted bowerbird *Chlamydera maculata*. *Emu* **92**, 11–18.
- Brockmann, J. H. & Barnard, C. J. 1979 Kleptoparasitism in birds. *Anim. Behav.* **27**, 487–514.
- Bushnell, P. J., Benignus, V. A. & Case, M. W. 2003 Signal detection behaviour in humans and rats: a comparison with matched tasks. *Behav. Proc.* **64**, 121–129.
- Chaffer, N. 1984 *In quest of bowerbirds*. New York: Rigby.
- Cooper, W. & Forshaw, J. 1977 *Birds-of-paradise and bowerbirds*. Sydney: Collins.
- Cuervo, J. J. & Møller, A. P. 1999 Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system. *Biol. J. Linn. Soc.* **68**, 505–529.
- Cuervo, J. J. & Møller, A. P. 2001 Components of phenotypic variation in avian ornamental and non-ornamental feathers. *Evol. Ecol.* **15**, 53–72.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: J. Murray.
- Diamond, J. 1987 Bower building and decoration by the bowerbird *Amblyornis inornatus*. *Ethology* **74**, 177–204.
- Donaghey, R. H. 1981 Use of time and space by breeding adult male satin bowerbirds *Ptilonorhynchus violaceus*. *Bird Behav.* **3**, 103.
- Frith, C. B. & Frith, D. W. 1994 Courts and seasonal activities at them by male tooth-billed bowerbirds, *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Mem. Queensland Mus.* **37**, 120–145.
- Frith, C. B., Frith, D. W. & Moore, G. J. 1994 Home range and extra-court activity in the male tooth-billed bowerbird, *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Mem. Queensland Mus.* **37**, 147–154.
- Giraldeau, L. A. & Beauchamp, G. 1999 Food exploitation: searching for the optimal joining policy. *Trends Ecol. Evol.* **14**, 102–106.
- Giraldeau, L. A. & Caraco, T. 2000 *Social foraging theory*. Princeton University Press.
- Ha, R. R. & Ha, J. C. 2003 Effects of ecology and prey characteristics on the use of alternative social foraging tactics in crows, *Corvus caurinus*. *Anim. Behav.* **66**, 309–316.
- Hunter, C. P. & Dwyer, P. D. 1997 The value of objects to satin bowerbirds *Ptilonorhynchus violaceus*. *Emu* **97**, 200–206.
- Hunter, F. M. & Davis, L. S. 1998 Female Adelie penguins acquire nest material from extrapair males after engaging in extrapair copulations. *Auk* **115**, 526–528.
- Iwasa, Y. & Pomiankowski, A. 1991 The evolution of costly mate preferences 2: the handicap principle. *Evolution* **45**, 1431–1442.
- Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. 2002 The sexual selection continuum. *Proc. R. Soc. Lond. B* **269**, 1331–1340. (DOI 10.1098/rspb.2002.2020.)
- Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. 2003 The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B* **270**, 653–664. (DOI 10.1098/rspb.2002.2235.)
- Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford University Press.
- Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3762.
- Lenz, N. 1994 Mating behavior and sexual competition in the regent bowerbird *Sericulus chrysocephalus*. *Emu* **94**, 263–272.
- McNamara, J. M., Webb, J. N., Collins, E. J., Székely, T. & Houston, A. I. 1997 A general technique for computing evolutionary stable strategies based on errors in decision-making. *J. Theor. Biol.* **189**, 211–225.
- Madden, J. R. 2002 Bower decorations attract females but provoke other male spotted bowerbirds: bower owners resolve this trade-off. *Proc. R. Soc. Lond. B* **269**, 1347–1351. (DOI 10.1098/rspb.2002.1988.)
- Madden, J. R. 2003 Bower decorations are good predictors of mating success in the spotted bowerbird. *Behav. Ecol. Sociobiol.* **53**, 269–277.
- Marshall, A. J. 1954 *Bowerbirds: their displays and breeding cycles*. Oxford University Press.
- Parker, G. A. 1983 Mate quality and mating decisions. In *Mate choice* (ed. P. Bateson), pp. 141–166. Cambridge University Press.
- Parker, G. A. 1984 Evolutionarily stable strategies. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 30–61. Oxford: Blackwell Scientific.
- Pomiankowski, A. & Møller, A. P. 1995 A resolution of the lek paradox. *Proc. R. Soc. Lond. B* **260**, 21–29.
- Pomiankowski, A., Iwasa, Y. & Nee, S. 1991 The evolution of costly mate preferences 1: Fisher and biased mutation. *Evolution* **45**, 1422–1430.
- Pruett-Jones, M. A. & Pruett-Jones, S. G. 1982 Spacing and distribution of bowers in Macgregor's bowerbird (*Amblyornis macgregoriae*). *Behav. Ecol. Sociobiol.* **11**, 25–32.

- Pruett-Jones, M. A. & Pruett-Jones, S. G. 1985 Food caching in the tropical frugivore, Macgregor's bower-bird (*Amblyornis macgregoriae*). *Auk* **102**, 334–341.
- Pruett-Jones, S. G. & Pruett-Jones, M. A. 1994 Sexual competition and courtship disruptions: why do male bowerbirds destroy each others bowers? *Anim. Behav.* **47**, 607–620.
- Rowland, W. J. 1994 Proximate determinants of stickleback behaviour: an evolutionary perspective. In *The evolutionary biology of the threespine stickleback* (ed. M. A. Bell & S. A. Foster), pp. 297–344. Oxford University Press.
- Schleicher, B., Valera, F. & Hoi, H. 1993 The conflict between nest guarding and mate guarding in penduline tits (*Remiz pendulinus*). *Ethology* **95**, 157–165.
- Shettleworth, S. J. 1998 *Cognition, evolution and behavior*. New York: Oxford University Press.
- Swaddle, J. P. 1999a Limits to length asymmetry detection in starlings: implications for biological signalling. *Proc. R. Soc. Lond. B* **266**, 1299–1303. (DOI 10.1098/rspb.1999.0778.)
- Swaddle, J. P. 1999b Visual signalling by asymmetry: a review of perceptual processes. *Phil. Trans. R. Soc. Lond. B* **354**, 1383–1393. (DOI 10.1098/rstb.1999.0486.)
- Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2000 Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching. *Proc. R. Soc. Lond. B* **267**, 251–256. (DOI 10.1098/rspb.2000.1994.)
- Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2001 Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *Am. Nat.* **158**, 530–542.
- Veselovsky, Z. 1978 Beobachtungen zu Biologie und Verhalten des Großen Kragenlaubenvogels (*Chlamydera nuchalis*). *J. Ornithol.* **119**, 74–90.
- Vickery, W. L., Giraldeau, L. A., Templeton, J. J., Kramber, D. L. & Chapman, C. A. 1991 Producers, scroungers, and group foraging. *Am. Nat.* **137**, 847–863.

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