Biological Journal of the Linnean Society, 2009, **96**, 372–382. With 2 figures

Why do females find ornaments attractive? The coercion-avoidance hypothesis

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Received 31 May 2008; accepted for publication 20 June 2008

Vertebrates show two major classes of sexually dimorphic traits: weaponry and ornaments. However, Darwin could not explain why their expression varies so much across lineages. We argue that coercion-avoidance can explain both the existence and taxonomic distribution of ornaments. Females maximize their fitness when they can freely choose their mates, but males are expected to use sexually dimorphic weaponry not only to displace other males, but also to overcome female preferences and thus acquire matings by force whenever they can. Females should therefore avoid coercive males and avoid using weaponry as a criterion for male quality wherever possible, and rely on male viability indicators that cannot be used to coerce females (i.e. ornaments). Ornaments predominate in birds and weaponry in mammals because female choice is less costly in birds, due to higher intrinsic female behavioural freedom and lower male monopolization potential. We also predict that specialized coercive organs occur where females have low behavioural freedom but males benefit little from weaponry in male–male contests. A review of the empirical evidence supports the basic predictions of this coercion-avoidance hypothesis. We also present a simple mathematical model that confirms the logic of this hypothesis. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **96**, 372–382.

ADDITIONAL KEYWORDS: behavioural freedom – female choice – intromittent organs – sexual selection – weapons.

INTRODUCTION

In many organisms, traits show sexual dimorphism (i.e. sex differences in their presence or expression). Darwin (1871) developed his theory of sexual selection to explain these sex differences. He recognized two main processes: competition for access to mates, usually most pronounced among males, and mate choice, usually most pronounced in females. Intrasexual competition explains sex differences in weaponry, whereas mate choice explains sex differences in ornamentation (Andersson, 1994). However, Darwin was puzzled by the relationship between these two components. As he amply documented (Darwin, 1871), birds are generally more ornamented than mammals, which in turn generally show greater development of weaponry. 'In the [. . .] chapter, on birds, a considerable body of direct and indirect evidence was advanced showing that the female selects her partner; and it would be a strange anomaly if female quadrupeds, which stand higher in the scale and have higher mental powers, did not generally, or at least often, exert some choice' (Darwin, 1871: 595). Yet, they generally do not, because 'with mammals the male appears to win the female much more through the law of battle than through the display of his charms' (Darwin, 1871: 570).

The main aim of the present study is to explain this basic contrast between birds and mammals. It is argued that females avoid using weaponry as indicators of male quality because weapons can be used to coerce them. Wherever multiple males are available to mate with a receptive female (e.g. because females invest heavily in offspring; Clutton-Brock & Parker, 1992) and females benefit from expressing a mating preference, conflict over the identity of mates arises. This will automatically lead to greater male persistence in mating attempts (harassment; Clutton-Brock & Parker, 1995) as well as attempts to force females to mate (sexual coercion; Smuts & Smuts, 1993), and also favour female counterstrategies.

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The coercion-avoidance hypothesis proposes that ornaments exist because females prefer to avoid using weapons as indicators of male viability. The hypothesis is based on two critical assumptions, which are reviewed below: (1) that both ornaments and weaponry reflect a male's intrinsic viability and (2) that females derive fitness benefits from being able to freely choose their mates. In principle, males are better off developing weaponry because this enhances their fighting ability but can simultaneously be used to coerce females, thereby avoiding rejection by females. Thus, weaponry will displace ornaments if females are unable to express their mating preferences at reasonable cost, and the presence of substantial sexual dimorphism in weaponry in a given lineage should thus reflect the situation in which females in this lineage have historically been unable to choose at low cost. In such situations, females may secondarily show a preference for weaponry, when preferred males protect them from harassment by nonpreferred males.

Males in many species nonetheless develop ornaments. We argue they do this because in these species females have enough freedom to escape mating attempts by nonpreferred males, and these males therefore derive no benefits from either success in male–male competition or attempts at coercion. Instead, they invest in structures that maximize their success at being selected as mates by freely choosing females, who derive fitness benefits from doing so.

We will first examine the evidence for the assumptions and the predictions of the hypothesis, and then specify, and subsequently model, the conditions in which weaponry (or specialized coercive organs) can displace ornaments.

MAIN ASSUMPTIONS OF THE COERCION-AVOIDANCE HYPOTHESIS

VIABILITY INDICATORS

Berglund, Bisazza & Pilastro (1996) defined 'armaments' as weapons and signals used in male–male competition (e.g. status badges). In the present study, we define weapons more specifically as sexually dimorphic traits that directly enhance the success in contest or combat and also include body size because mere body size also affects this success. We will refer to 'weapons' when referring to sexually dimorphic tusks, horns, antlers, spines, canines, spurs, sharp claws, and beaks, and to 'weaponry' whenever the argument applies to sexual dimorphism in body size as well.

Ornaments are features that do not directly increase fighting ability. We define ornaments as sexually dimorphic traits attractive to the opposite sex (rather than 'preferred' by females, as defined in Berglund *et al.*, 1996, where preference can be expressed as a result of male use of force). In the present study, we are mainly interested in morphological ornaments, such as combs, wattles, protuberances, plumes, lengthened feathers, elongated tails, and brightly coloured beaks or patches of fur, feathers, or skin. However, vocal and instrumental songs calls or courtship displays that attract the opposite sex can also be regarded as ornaments (Darwin, 1871; Andersson, 1994). Ornaments or weapons can also take the form of chemical or electrical signals without affecting these definitions (Berglund *et al.*, 1996).

Theory suggests (Grafen, 1990) and empirical results confirm (Jennions, Møller & Petrie, 2001) that males with larger ornaments, weapons, or body size, and with higher rates of courtship or larger song repertoires have increased resistance to parasites or disease and greater survivorship and longevity, in spite of the investment of time and energy (Walther & Clayton, 2005), the need for specific or rare nutrients (Geist, 1966, 1986), increased risk of predation (Møller & Nielsen, 1997), interference with the efficiency of foraging (Matyjasiak *et al.*, 1999) or flight (Møller & Hedenstrom, 1999), or injury or death during fights over territories or females (Andersson & Iwasa, 1996). Thus, the size of both ornaments and weaponry reflect a male's intrinsic viability ('good genes') (Scribner, Smith & Jones, 1989; Scribner & Smith, 1990; Andersson, 1994; Fitzsimmons, Buskirk & Smith, 1995; Berglund *et al.*, 1996; Brown, 1997; Kokko *et al.*, 2003).

We assume that the relationship between size of a structure and male viability is equal for weaponry and ornaments, so that a female selecting males based on one or the other always ends up selecting males based on intrinsic viability. It is difficult to test this assumption directly (Promislow, Montgomerie & Martin, 1992). However, ornaments and weapons show similar allometric relationships with body size across species (Kodric-Brown, Sibly & Brown, 2006), suggesting that the relationship between viability and expression of these two different secondary sexual traits is similar. Thus, whenever males invest exclusively in one or the other, females should derive equal benefit from preferring the largest weaponry and the largest ornaments (ignoring coercion).

THE ADAPTIVE NATURE OF FEMALE MATE CHOICE

Several hypotheses have been proposed to explain the evolution and maintenance of female mating preferences (Kokko *et al.*, 2003). The benefits gained by females from biased matings may be a direct increase in fecundity or access to resources, or indirect, in that their sons will be more attractive as mates (known as the Fisher–Zahavi model: Eshel, Volovik & Sansone (2000). The female mating preference is maintained if both a male's reproductive success and the size of its signal continue to increase with his quality, despite signal cost. Even if female mate choice for males with certain traits evolved as a result of exploitation of pre-existing sensory biases among females, there is still selection on female preferences because females benefit from the production of more attractive sons (Kokko *et al.*, 2003).

We therefore expect females to choose mates whenever possible and thereby accrue fitness benefits. Several experiments demonstrate that females paired to males they find attractive produced more offspring (Møller & Thornhill, 1998; Paul, 2002; Persaud & Galef, 2005a, b). Moreover, in both house mice (*Mus musculus*) and mallards (*Anas platyrhynchos*), not only the number of offspring, but also their viability was significantly lower when a female reproduced with their nonpreferred partner than with their preferred partner (Drickamer, Gowaty & Holmes, 2000; Bluhm & Gowaty, 2004). Similarly, in pronghorn (*Antilocapra americana*), which have singletons, free mate choice produced more viable offspring than experimentally induced random mating (Byers & Waits, 2006).

MAIN PREDICTIONS OF THE COERCION-AVOIDANCE HYPOTHESIS

In the present study, we examine three main predictions of the coercion-avoidance hypothesis. The first prediction follows directly from the presence of adaptive female mate preferences. Nonpreferred males are expected to use their weaponry to coerce females into mating whenever they can. Smuts & Smuts (1993) and Clutton-Brock & Parker (1995) review the abundant evidence for use of weaponry by male mammals in harassment and sexual coercion, potentially leading to injuries or even death (Mesnick & LeBoeuf, 1991; Reale, Bousses & Chapuis, 1996). Evidence for forced matings in turtles is likewise found in those species where males are lager than females (Berry & Shine, 1980). Also, as expected, females actively avoid mating with males that harass or force them (Persaud & Galef, 2005a).

The second prediction is that cases in which ornamented males successfully coerce females into mating with them must be very rare. By contrast to the large literature on sexual coercion in mammals, there are few reports of males in ornamented bird species coercing females into mating with them. Westneat (1987), McKinney & Evarts (1997) and Gowaty & Buschhaus (1998) summarize the relatively few known cases. In all of them, however, females resist and escape, thus considerably reducing the chances of fertilization, except where females cannot escape (e.g. some captive settings; Ophir, Persaud & Galef, 2005), or in species where males possess unusual intromittent organs (McKinney & Evarts, 1997; Low, 2005). It is remarkable that, even where male birds are much larger, they appear to refrain from coercion attempts (Göransson *et al.*, 1990). Thus, in ornamented birds, the female's escape potential tends to be high.

The third, and most critical prediction is that, in species where females can still express their preferences but males also have weaponry, females either ignore weaponry and rely exclusively on ornaments in their mate choice or actually express choice against males with weaponry. In the present study, we examine three cases where males possess weapons: (1) pheasants, where males possess weapons as well as ornaments (rare in birds); (2) lekking ungulates with weaponry, where females can express choice freely (rare in mammals); and (3) raptors, where both males and females possess lethal weapons but females are larger than males on average. If possible, we present the results of experiments that created conditions for females to express their choice freely, rather than rely on observations of matings.

Males of 85% of the species of the Phasianidae (Davison, 1985) have a bony spur on the tarsometatarsus. Spurs are generally used in fighting (Davison, 1985; Andersson, 1994; Mateos & Carranza, 1995) but their use as cues by females is debated. In the pheasant, *Phasianus colchicus*, males are on average 50% heavier than females and more brilliantly coloured, have a longer tail and have a large spur on each tarsus (Göransson *et al.*, 1990). They have a polygynous mating system, but females move freely through territories and visit different territorial males and males cannot prevent them from doing so. As a result, there is an intense intrasexual competition as well as female mate choice (Mateos, 1998), which explains the presence of the weapon (spurs) alongside various ornaments.

In experimental field studies, Von Schantz *et al.* (1989) and Von Schantz, Grahn & Göransson (1994) showed that male viability is correlated with spur length and that females prefer long-spurred males, even if the effect of male body size is controlled for statistically. In addition, Göransson *et al.* (1990) showed that spur length of males was the most important correlate of harem size. These results suggest that females select males based on spur length. However, in another experimental study (Grahn, Göransson & von Schantz, 1993), groups of males with different spur lengths, but otherwise similar in body measurements and age distribution, did not differ significantly in attracting females. Similarly, Mateos & Carranza (1996) could not show any female preference for experimentally manipulated spur lengths in captive ring-necked pheasants (*P. colchicus*). Instead, spur length was correlated with ornamental characteristics such as length of ear tufts and the presence of black points in the wattle, which were preferred by females (Mateos & Carranza, 1995, 1996). Buchholz (1995) showed that female wild turkeys in captivity preferred ornamented males with longer snoods and wider skullcaps and that spur length did not explain female choice of mates. Thus, these other studies argue that females do not use spur size as a criterion for mate choice. Importantly, although Von Schantz *et al.* (1989) strongly support the role of spur length in female choice of mates, nevertheless, they too suggest that several male ornaments may be involved in female choice (Von Schantz *et al.*, 1994). Thus, even if there is no direct evidence that females actively avoid matings with males with larger spurs, the experiments indicate that females generally rely on ornaments.

In lek mating systems, males advertise themselves to females with elaborate visual, motor, acoustic or olfactory displays, and females visit leks solely to mate (Bradbury, 1981). Clearly, female choice can be expressed in this type of mating system (Clutton-Brock *et al.*, 1988; Höglund, Montgomerie & Widemo, 1993). Lekking is rare in mammals. Studies showed that female ungulates experience lower risk of damaging harassment by males on leks than elsewhere (McComb & Clutton-Brock, 1994; Nefdt, 1995; Carranza & Valencia, 1999), explaining why lekking males are preferred, despite the presence of weapons. Nonetheless, in fallow deer (*Dama dama*), does do not move to larger bucks or to those with larger antlers (Clutton-Brock, Hiraiwa-Hasegawa & Robertson, 1989), but preferred males with larger harems (Fitzsimmons *et al.*, 1995). Similarly, in blackbucks (*Antilope cervicapra*), there is no correlation between horn characteristics and measures of female preference (female visits, courtship rates, matings; K. Isvaran, unpublished data, pers. comm.). The red deer (*Cervus elaphus*) is not a lekking species, but females collect in mating areas containing several rutting males defending females along with territories that contain resources used by females (Carranza, 1995; Carranza & Valencia, 1999). Hinds do not select mates on the basis of their antler size (Clutton-Brock, 1982), but may prefer roars of larger males that provide better protection from harassment by other males (Charleton, Reby & McComb 2007). Thus, despite the protection against harassment or coercion by nonpreferred males offered by males with greater weaponry, these female ungulates never appear to use weaponry itself as a mate choice criterion.

The third case in which males possess weapons are birds of prey. In most birds of prey, including hawks (Falconiformes), owls (Strigiformes), and skuas and jaegers (Stercorariidae, Charadriiformes), females are larger than males, sometimes substantially so (Amadon, 1959, 1975; Andersson, 1994), and therefore also have larger weapons. Numerous hypotheses have been suggested to explain this (Andersson & Norberg, 1981). The raptors possess lethal weapons: sharp, curved, pointed talons, and a hooked formidable beak. The reverse size dimorphism in raptors is greatest in species that pursue, kill and rend large, active prey; less in those that kill small rodents or insects; and absent or virtually so in vultures, known to be dull-clawed (Amadon, 1975). Similarly, skuas and jaegers have both very sharp curved claws and reverse dimorphism, whereas the closely-related gulls lack talons and have normal dimorphism (Smith, 1982).

Various explanations have been proposed. First, although female raptors are bigger than males, they neither compete more intensively for mates than males, nor have reversed parental care roles (Amadon, 1975), excluding sex role reversal. A second interpretation is ecological: smaller prey are more abundant than larger prey and smaller raptors capture prey more frequently than larger ones (Safina, 1984; Krüger, 2005). Although this may be the case, only the coercion-avoidance hypothesis can explain why females are especially larger than males in species with more dangerous weapons. Other hypotheses are consistent with the coercion-avoidance hypothesis. Amadon (1975) suggests that because, in most raptors, males are territorial and attack intruders, selection would favour greater physical prowess in the female to reduce risk of injury. Smith (1982) agreed, but also posited advantages of breeding female dominance.

The coercion-avoidance hypothesis also predicts that females should specifically choose males that are smaller than themselves whenever possible. In an experimental study of kestrels, Hakkarainen *et al.* (1996) indeed showed that females preferred lighter males with shorter tarsi as mates, at least when the difference in those characters between competing males was greater than average. Likewise, in skuas and jaegers, small females avoid pairing with large males (Catry, Phillips & Furness, 1999). Finally, female Tengmalm's owls have been shown to choose light, short-winged males (Korpimaki, 1986).

These three cases show that females either select against males with larger weapons (as in the birds of prey) or are indifferent to weaponry. In general, if males never use their weapons to coerce females into mating with them, there is no need for active female discrimination against male weaponry. There was only a single example (Von Schantz *et al.*, 1994) of females using the size of male weaponry as an indicator of viability, but subsequent studies questioned this conclusion. These findings thus indicate that the third prediction is met. In general, support for the three predictions is strong enough to establish the plausibility of the coercion-avoidance hypothesis.

MODELLING THE EVOLUTION OF ORNAMENTS AND WEAPONRY

CONDITIONS FAVOURING ORNAMENTS OR WEAPONRY

The coercion-avoidance hypothesis assumes that ornaments will predominate wherever females are free to choose, whereas weaponry will predominate where a female's costs of refusing to mate with males (and thus of exerting their mate preferences) are too high relative to the benefit of mating with a preferred male. High costs arise when: (1) females have low intrinsic female escape ability and (2) females are clumped, thus creating a high monopolization potential for the male.

The first condition favouring weaponry is where nonpreferred males can overcome female mating preferences, or can make it very costly for the female to refuse mating. This applies when a female has an intrinsically low escape potential or mobility relative to the male, due to a combination of habitat, locomotor biology, and the presence of pre-existing organs that can be used to coerce females (such as hands in mammals, or claws used to catch prey in birds). The natural history of this condition is examined in the Discussion.

Second, when females are clumped in space and have relatively low mobility, one male can potentially defend access to multiple females. An increase in male weaponry is thus expected where the high potential for polygynous matings increases the benefits of excluding other males. Likewise, it is expected when a dominant male manages to exclude other males from the females; a female who successfully refuses to mate with a nonpreferred male who monopolizes access to her incurs additional losses because she will have to locate another male. This condition is most likely to apply to taxa in which males do not contribute to parenting, and therefore can respond to situations with a high monopolization potential. In addition, it is most likely when females are clumped in space, as in many diurnal mammals (Alexander, 1974).

THE MODEL

Here, we build a formal model. The model assumes that females are primary caretakers. If they are not, controlling the identity of their mates affects fitness far less. We also assume that a male maximizes his fitness either by attracting a female through ornaments (the amount of ornamentation developed by a male is measured here as A_o) or by excluding other males and/or sexual coercion (measured here as A_f) through weapons (i.e. fighting ability). We assume that both strategies require similar energy inputs. Similarly, we assume that the female maximizes her fitness when she can choose her preferred mates, as reviewed above.

Assuming linear tradeoffs between ornaments and weapons, we write the normalized male fitness as:

$$\text{Fitness} = \Delta \times A_o + (1 - \Delta) \times A_f \tag{1}$$

where A_o and A_f are both normalized between 0 and 1. We have denoted a female's ability to avoid mating by Δ. For $\Delta = 0$, the female cannot avoid the mating and thus male fitness is entirely dependent on A_f. At $\Delta > 0$, she can do so at a lower cost until, at $\Delta = 1$, the female is always successful in avoiding mating at a minimal cost, and male fitness depends entirely on A_o. We know that A_f has two components (i.e. male–male competition and the male's ability to coerce the female). However, because the outcome of male–male competition is dependent on how skewed male mating success is, we propose a simple expression for A_f as:

$$A_f = \beta \times \sigma + (1 - \beta) \times C \tag{2}$$

where

$$C = \gamma\sigma \tag{3}$$

In eqns (2) and (3), σ is the male–male fighting ability (normalized between 0 and 1, proportional to the development of weaponry), C is the ability to coerce the female so that she mates with the male (it is the partial use of weapons in forcing the female; we assume γ to be a small constant between 0 and 1 because the male is not expected to injure the female intentionally), and β is the environmentally imposed degree of despotism among males. When $\beta = 0$, there is a complete scramble among males, whereas when $\beta = 1$, the dominant male monopolizes all the matings (for a definition of β, see Pandit & van Schaik, 2003; van Schaik, Pandit & Vogel, 2005). An intrinsic assumption of expression (2) is that coercion is neither needed nor useful when β is very high, but will be useful when β is low.

The female can avoid forced matings by using her natural freedom weighted by the cost in terms of energy and time invested in searching for another mate. We propose that such a cost will be dependent on β so that if β is high (i.e. dominant male drives away all the other males), it is less effective for a female to resist mating since the cost of finding another mate will be very high. Hence, we hypothesize that her ability to avoid mating will be:

$$\Delta = \delta(1 - \beta)^{\alpha} \tag{4}$$

where α ($0 \leq \alpha \leq 1$) determines the magnitude of the dependence on β. For $\alpha = 0$, the female's ability to avoid mating (i.e. Δ), equals her intrinsic natural ability to escape (i.e. δ) so that β plays no role, whereas when $\alpha = 1$, the female's ability to avoid mating is dominated by β. When there is complete monopolization (i.e. $\beta = 1$) and all other males are excluded by the dominant, Δ will effectively be zero because females may have great difficulty travelling to other males, even if their direct ability to select mates is high. In natural settings, we expect α to take some fixed value between zero and one, depending on environmental conditions.

The size of ornaments and weapons directly reflects male quality. We also assume that the male's expenditure on the development of ornaments and weapons directly trade off against each other. Hence, we express his internal quality (q) as a simple linear combination of these two quantities:

$$q = \sigma + A_o \tag{5}$$

With the linear trade-off between them, we assume that there is a linear relationship between investment in each of them and male fitness. In addition, we assume that male quality (q) is constant across males. Whereas none of the assumptions are likely to hold fully, we do not expect qualitative differences when they are relaxed and the model is made concomitantly more complex.

In this analysis, we also assume that the parameters β and δ are set by external conditions. In practice, of course, they change over time, in part due to antagonistic evolution between the sexes. In general variation in δ is in evolutionary time. However, β can exhibit large fluctuations due to change in environment and/or group size. This is relevant because once weaponry is established it may not be possible for the system to revert if β is reduced again later.

Combining eqns (1) to (5), we write male fitness as a function of four parameters A_o, σ, β, and δ. Because β and δ are set by environmental conditions, and are therefore not under immediate control of the male, we assume that in an evolutionary process, natural selection will change the male's A_o and σ so as to achieve maximum fitness, while keeping environmental conditions and male quality constant.

MODEL RESULTS

Figure 1 depicts the regions of β–δ space where males maximize their fitness by developing ornaments (white region) or weaponry (dark region). Males are shown to maximize their fitness by investing in ornaments when δ is high and β is low, whereas investment in weaponry brings maximum fitness when δ is low and β is high. Figure 1 demonstrates the effect of low and high effectiveness of weaponry in sexual coercion [γ in eqn. (3)], respectively. Interestingly, this effectiveness determines the value of δ at which males are expected to start investing in ornaments rather than weaponry. The plot is for $\alpha = 0.5$, but the qualitative result holds irrespective of the values of α. Strengthening the negative impact of male exclusion of other males on the female's ability to find other mates (i.e. $\alpha \rightarrow 1$) reduces the zone where ornaments are the best investment decision toward much higher values of δ, and comparatively lower values of β. In other words, high levels of ornamentation are expected where females cannot be forced, more or less regardless of the monopolization potential for the males, unless that makes it impossible for females to find other males. Weaponry, instead, is found, where

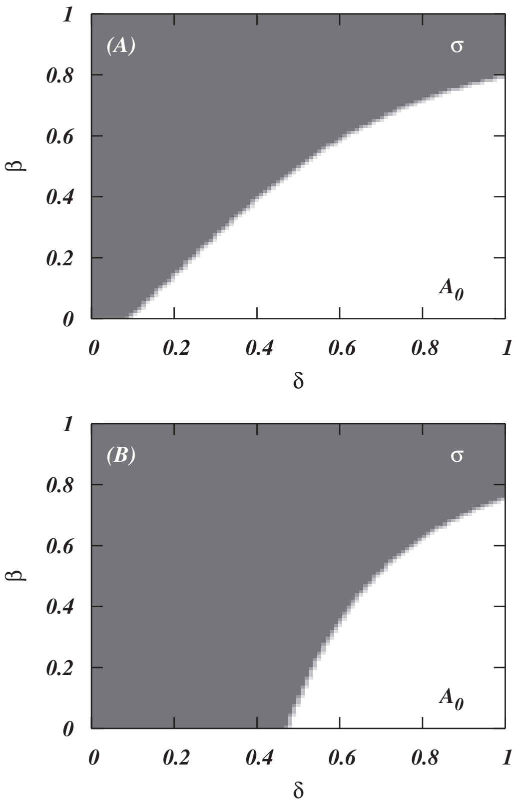

Figure 1. Regions in β–δ space where the male's fitness is maximum if he develops ornaments (white region, marked by A_o) or weapons (dark grey region, marked by σ) at a moderate value of α ($\alpha = 0.5$) for (A) low value of γ ($\gamma = 0.1$) (B) for very high value of γ ($\gamma = 0.9$) where α indicates the negative impact of male exclusion of other males on the females' ability to find other mates and γ indicates the intensity of male sexual coercion through available weaponry. It is illustrated that as γ gets stronger, it is advantageous for the male to invest in ornaments only at higher values of δ.

females have only moderate escape ability and males can also monopolize them against other males.

ADDING COERCIVE ORGANS

What happens if males develop nonweapon coercive organs? These can be defined as features that are sexually dimorphic and function to subdue or force the female to mate, but do not improve success in male–male combat, nor raise the possessor's attractiveness to the opposite sex. Coercive organs differ from weaponry in that weaponry may often serve both in male–male contests and mate coercion (with effectiveness γ), whereas coercive organs themselves are (by definition) unable to provide benefits in contests with other males, although some secondary usage in male–male competition may occur (Arnqvist & Rowe, 2005: 65, 67). By making female choice more difficult, coercive organs obviate the use of ornaments as criteria for mate choice by females.

Coercive organs come in two general forms: grasping organs and intromittent organs. If males have specialized grasping structures, these can be used both before and during mating to overcome female resistance. Examples include antennal claspers in water striders, notal organs in scorpion flies, and modified walking legs in crustaceans (Arnqvist & Rowe, 2005). Intromittent organs can be used to make matings more effective. They are ubiquitous among mammals and almost ubiquitous among reptiles, but their presence varies among birds (King, 1981; Briskie & Montgomerie, 1997).

The high cost of producing and maintaining weaponry and ornaments results in a direct relationship between their size and the intrinsic viability of their owners. We assume that this relationship does not hold for intromittent organs (such as a penis) because their effectiveness probably does not increase beyond a certain size and their size does not vary much among males, unlike ornaments and weaponry (Anderson, 2000). Grasping structures, on the other hand, may be as large as possible, because one expects a positive relationship between size and effectiveness. The model therefore does not apply to grasping organs (but see the Discussion).

To study the effect of nongrasping coercive organs on male fitness, we first modify eqn. (3):

$C = \gamma\sigma$ in the absence of coercive organs
$C = 1$ in the presence of coercive organs

which means that coercion resulting from coercive organs is the most effective.

Now, we can ask under what conditions males benefit from developing coercive organs in addition to weaponry or ornaments (which of these is present depending on their position in β–δ space). As shown in Figure 2, the presence of coercive organs makes a strong contribution to male fitness especially when both β and δ are low. Thus, given some finite cost to developing coercive organs, the model predicts that coercive organs are more likely to evolve when: (1) females have limited intrinsic escape ability (δ), due to some biological constraint or due to special circumstances and, simultaneously, (2) monopolizability (β) is low so that weapons are of little use in male-male contests, for example because females are scattered in space or highly seasonal or cryptic breeders.

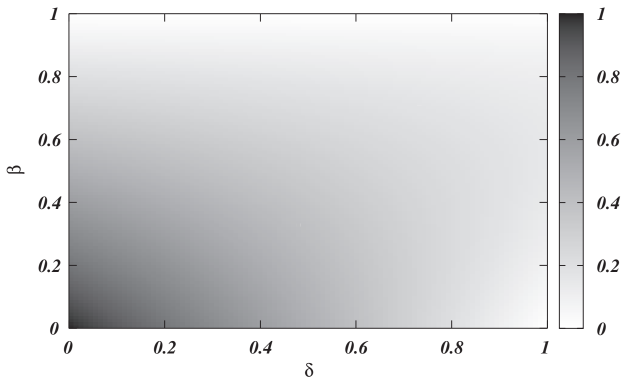

Figure 2. For fixed parameter values, fitness difference in β–δ space, in presence and absence of coercive organs. The figure clearly shows that additional presence of coercive organs makes a very strong contribution to male fitness mostly in the region where both β and δ are small (lower left corner).

Because the presence of coercive organs renders ornaments less effective, we should expect fewer ornaments in the lower β–δ space whenever coercive organs are possible. The effect of coercive organs on weaponry is probably smaller, so they should frequently coexist.

DISCUSSION

THE MODEL'S PREDICTIVE ABILITY

We developed a mating conflict model for the distribution of weaponry, ornaments and coercive organs. According to the model, ornaments will predominate where females have high escape potential, weaponry will predominate where females have low escape potential and males simultaneously have a high monopolization potential, whereas coercive organs appear where both female escape potential and male monopolization potential are low.

Coercive organs come in two main varieties: intromittent and grasping organs. The present model deals only with intromittent organs, whose effectiveness is largely independent of size. Grasping organs, however, may be more like weapons and ornaments in that larger size may mean greater effectiveness. If we rebuild the model to make grasping organs a third target of male investment, equal to weaponry and ornaments, these kinds of coercive organs predominate in the same region in β–δ space as intromittent organs of fixed size, but their size will trade off against that of ornaments. Thus, species with grasping organs whose size depends on a male's intrinsic viability should show a lower investment into male ornamentation. We have not tested this prediction further.

The coercion-avoidance hypothesis reproduces the general difference between birds and mammals. Birds are more ornamented than mammals because female birds have greater intrinsic freedom to escape from males attempting to harass them. Male mammals are more likely to have weaponry because of both the lower escape ability of females and the generally higher monopolization potential. The hypothesis thus solves Darwin's puzzle of the bird–mammal contrast in ornamentation and weaponry. It also accounts for other contrasts between the two lineages, such as the rarity of forced matings and the disappearance of penises in birds, and the absence of building female-attracting structures and the rarity of lekking in mammals despite the low male participation in parental care and thus apparent feasibility of lekking. Finally, it can also account for seemingly unrelated phenomena such as reversed sexual dimorphism in raptors (Amadon, 1975; Krüger, 2005) or the covariation between sexual dimorphism and use of displays among turtles (Berry & Shine, 1980). Future work should develop more precise predictions in lineages with variable expression of weaponry, ornamentation, and coercive organs, based on quantitative estimates of female behavioural freedom and male monopolization potential.

ALTERNATIVE HYPOTHESES

Berglund *et al.* (1996) suggested that weapons and ornaments arose first as indicators of males' fighting ability in male contests, but then were subsequently used by females as indicators of intrinsic male quality. Our hypothesis does not preclude the use by males of ornaments as indicators of fighting ability in male–male contests. There is abundant evidence that they do so in many species (Andersson, 1994; Berglund *et al.*, 1996). Nor does our hypothesis preclude the use by females of male ornaments to assess male viability. However, Berglund *et al.* (1996) review actually yielded virtually no cases where females use male weaponry as an indicator of male viability.

Eberhard (2002) argues that male persistence and forcefulness prior to intromission does not qualify as sexual coercion, rather it is a female's way of testing male's quality. However, this alternative interpretation of male coercion is refuted for the species in which offspring number and viability were greater for females who could mate with their preferred male (Gowaty, 2004). Moreover, if Eberhard's (2002) hypothesis applies universally, then ornaments should never evolve in any taxon, contrary to what is observed in nature. This same objection holds for a modified version (Cordero & Eberhard, 2003; Eberhard, 2005), which claims that the costs imposed on females by male coercion are less than the (temporary) benefits gained by females from having coercive sons (in a population of mostly noncoercing males).

FEMALE BEHAVIOURAL FREEDOM

Female behavioural freedom or escape ability (Gowaty, 1997, 2004; Caizergues & Lambrechts, 1999) was identified as a critical variable. A female's escape potential depends on the interaction between habitat and biology. We suggest that the ability to freely move in three dimensions, such as air (flight) or water (swimming under water), or even forest canopy (climbing and leaping), increases the female's escape ability relative to the two-dimensional terrestrial habitat. There are four lines of evidence to support this suggestion.

First, the evolution of flight was probably accompanied by a dramatic increase in female behavioural freedom, resulting in the loss of coercive organs such as the penis (present in reptiles; King, 1981) and an increase in ornamentation through the expression of female mating preferences. Penises would have re-evolved in those bird lineages where females had lower escape potential due to unusual ecological conditions or newly-evolved predisposing factors. Forced matings involving coercive organs are concentrated in non-arboreal birds that are also tied to highly localized critical resources, such as ponds, forcing them to be present in essentially two-dimensional habitats (McKinney & Evarts, 1997). One of the rare examples of forced copulations involving active female resistance in arboreal birds comprises the New Zealand stitchbird, *Notiomystis cincta*. Males of this species have very large penis-like cloacal protuberances that help him to eliminate female control (Low, 2005). Males of all flightless birds (ratites and tinamous) have penises, probably retained from their common ancestor, but all show exclusive or predominant male parental care of eggs and young (Handford & Mares, 1985; Davies, 2002). Second, in turtles, among aquatic taxa males display to females and mate when chosen by females, whereas among semi-aquatic and, especially, bottom-walking taxa, males force matings (Berry & Shine, 1980). Third, among insects, grasping organs are widespread among water striders

(Arnqvist & Rowe, 2005), which live on the water's surface, a two-dimensional habitat. Fourth, among primates, females of arboreal species tend to be better able to resist forced matings (Smuts & Smuts, 1993), with the exception of orang-utans (Fox, 2002), who do not leap and always use multiple supports, making it possible for males and to approach and restrain them. In conclusion, coercive grasping organs are more likely where lower mobility or habitat constraints limit female behavioural freedom.

WEAPONRY: COMBAT AND COERCION?

The textbook explanation for sexual dimorphism in body size and weapons, especially among mammals, is that they evolved through intrasexual selection (Alcock, 2001). There have been various suggestions for the exceptions to the rule that contest for mating access is accompanied by increased size of male weaponry. For example, males could increase success in contests by being more agile (e.g. equids: Rubenstein, 1986); turtles: (Andersson, 1994: 268). Similarly, the greater dimorphism in terrestrial than arboreal primates with similar group composition (Clutton-Brock, Harvey & Rudder, 1977; Plavcan & van Schaik, 1997) has been attributed to limitations on size increases in an arboreal niche. An additional possibility, however, is that weaponry serves to overcome female resistance and force females into mating. In other words, sexual dimorphism in body size and weapons may have both an intrasexual selection and a mating conflict component.

This suggestion is not new (Ghiselin, 1974; Berry & Shine, 1980; Shine & Mason, 2005) but has not been tested systematically so far. It can easily account for the broad difference between snakes and lizards in sexual dimorphism in body size. Snakes lack grasping organs, and females are larger than males in most species (Shine, 1978), whereas the opposite is true in lizards (Darwin, 1871), where males can grasp females with their extremities. Where males can grasp females, there may often be selection on them to grow bigger than females, whereas this pressure is absent where males cannot. Similarly, if male coercion is easier in (quadrumanous) terrestrial than arboreal species, the increased weaponry of male primates in terrestrial species (van Schaik, Hodges & Nunn, 2000) could be linked to the success it brings in overcoming female defences. Thus, a fresh look at the selective agents responsible for weaponry may be productive.

ACKNOWLEDGEMENTS

We would like to thank Parry Clarke, Patricia Gowaty, Charlie Nunn, and Maria van Noordwijk for their helpful and constructive comments on the earlier draft of the manuscript; Sagar Pandit and Bob Trivers for stimulating discussions; and two anonymous reviewers for useful feedback.

REFERENCES

Alcock J. 2001. *Animal behavior*. Sunderland, MA: Sinauer Associates, Inc.

Alexander RD. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* **5:** 325–383.

Amadon D. 1959. The significance of sexual differences in size among birds. *Proceedings of the American Philosophical Society* **103:** 531–536.

Amadon D. 1975. Why are female birds of prey larger than males? *Journal of Raptor Research* **9:** 1–11.

Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Anderson MJ. 2000. Penile morphology and classification of bush babies (Subfamily Galagoninae). *International Journal of Primatology* **21:** 815–836.

Andersson M, Iwasa Y. 1996. Sexual selection. *Trends in Ecology and Evolution* **11:** 53–59.

Andersson M, Norberg R. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* **15:** 105–130.

Arnqvist G, Rowe L. 2005. *Sexual conflict*. Princeton, NJ: Princeton University Press.

Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* **58:** 385–399.

Berry JF, Shine R. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia* **44:** 185–191.

Bluhm CK, Gowaty PA. 2004. Social constraints on female mate preferences in mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Animal Behaviour* **68:** 977–983.

Bradbury JW. 1981. The evolution of leks. In: Alexander RD, Tinkle TW, eds. *Natural selection and social behaviour*. New York, NY: Carron Press, 138–169.

Briskie JV, Montgomerie R. 1997. Sexual selection and the intromittent organ of birds. *Journal of Avian Biology* **28:** 73–86.

Brown JL. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology* **8:** 60–65.

Buchholz R. 1995. Female choice, parasite load and male ornamentation in wild turkeys. *Animal Behaviour* **50:** 929–943.

Byers JA, Waits L. 2006. Good genes sexual selection in nature. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 16343–16345.

Caizergues A, Lambrechts MM. 1999. Male 'macho' mammals exploiting females versus male 'Don Juan' birds exploited by females: the opposite-sex exploitation (OSEX) theory. *Ecology Letters* **2:** 204–206.

Carranza J. 1995. Female attraction by males versus sites in territorial rutting red. *Animal Behaviour* **50:** 445–453.

Carranza J, Valencia J. 1999. Red deer females collect on male clumps at mating areas. *Behavioral Ecology* **10:** 525–532.

Catry P, Phillips RA, Furness RW. 1999. Evolution of reversed sexual size dimorphism in skuas and jaegers. *The Auk* **116:** 158–168.

Charleton BD, Reby D, McComb K. 2007. Female red deer prefer the roars of larger males. *Biology Letters* **3:** 382–385.

Clutton-Brock TH. 1982. The function of antlers. *Behaviour* **79:** 108–125.

Clutton-Brock TH, Parker GA. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Reviews in Biology* **67:** 437–456.

Clutton-Brock TH, Parker GA. 1995. Sexual coercion in animal societies. *Animal Behaviour* **49:** 1345–1365.

Clutton-Brock TH, Harvey PH, Rudder B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* **269:** 58–60.

Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Albon SD. 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology* **23:** 281–296.

Clutton-Brock TH, Hiraiwa-Hasegawa M, Robertson A. 1989. Mate choice on fallow deer leks. *Nature* **340:** 463–465.

Cordero C, Eberhard WG. 2003. Female choice of sexually antagonistic male adaptation. sa critical review of some current research. *Journal of Evolutionary Biology* **16:** 1–6.

Darwin C. 1871. *The descent of man and selection in relation to sex*. London: John Murray.

Davies SJJF. 2002. *Ratites and Tinamous*. Oxford: Oxford University Press.

Davison GWH. 1985. Avian spurs. *Journal of Zoology London (A)* **206:** 353–366.

Drickamer LC, Gowaty PA, Holmes CM. 2000. Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Animal Behaviour* **59:** 371–378.

Eberhard WG. 2002. The function of female resistance behavior: intromission by male coercion vs. female cooperation in sepsid flies (Diptera: Sepsidae). *Revista de Biologia Tropical* **50:** 485–505.

Eberhard WG. 2005. Evolutionary conflicts of interest: are female sexual decisions different? *American Naturalist* **165:** S19–S25.

Eshel I, Volovik I, Sansone E. 2000. On Fisher–Zahavi's handicapped sexy son. *Evolutionary Ecology Research* **2:** 509–523.

Fitzsimmons N, Buskirk SW, Smith MH. 1995. Population history, genetic variability and horn growth in Bighorn sheep. *Conservation Biology* **9:** 314–323.

Fox E. 2002. Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology* **52:** 93–101.

Geist V. 1966. Evolutionary significance of mountain sheep horns. *Evolution* **20:** 558–566.

Geist V. 1986. The paradox of the Great Irish Stags. *Natural History* **3:** 54–64.

Ghiselin MT. 1974. *The economy of nature and the evolution of sex*. Berkeley, CA: University of California Press.

Gowaty PA. 1997. Sexual dialectics, sexual selection, and variation in mating behavior. In: Gowaty PA, ed. *Feminism and evolutionary biology: boundaries, intersections, and frontiers*. New York, NY: Chapman Hall, 351–384.

Gowaty PA. 2004. Sex roles, contests for the control of reproduction, and sexual selection. In: Kappeler P, van Schaik CP, eds. *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press, 37–54.

Gowaty PA, Buschhaus N. 1998. Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy. *American Zoologist* **38:** 207–225.

Grafen A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* **144:** 517–546.

Grahn M, Göransson G, von Schantz T. 1993. Territory acquisition and mating success in pheasants, *Phasianus colchicus*: an experiment. *Animal Behaviour* **46:** 721–730.

Göransson G, von Schantz T, Froberg I, Helegee A, Wittzell H. 1990. Male characteristics, viability and harem size in the pheasant *Phasianus colchius*. *Animal Behaviour* **40:** 89–104.

Hakkarainen H, Huhta E, Lahti K, Lundvall P, Mappes T, Tolopen P, Wiehn J. 1996. A test of male mating and hunting success in the kestrel: the advantage of smallness? *Behavioral Ecology and Sociobiology* **39:** 375–380.

Handford P, Mares MA. 1985. The mating systems of ratites and tinamous: an evolutionary perspective. *Biological Journal of the Linnean Society* **25:** 77–104.

Höglund J, Montgomerie R, Widemo F. 1993. Costs and consequences of variation in the size of ruff leks. *Behavioral Ecology and Sociobiology* **32:** 31–39.

Jennions MD, MØller AP, Petrie M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Quarterly Review of Biology* **76:** 3–36.

King AS. 1981. Phallus. In: King AS, McLelland J, eds. *Form and function in birds*, Vol. 2. London: Academic Press, 107–147.

Kodric-Brown A, Sibly RM, Brown JH. 2006. The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 8733–8738.

Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270:** 653–664.

Korpimaki E. 1986. Reversed size dimorphism in birds of prey, especially in Tengmalm's owl *Aegolius funereus*: a test of the 'starvation hypothesis'. *Ornis Scandinavica* **17:** 326–332.

Krüger O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evolutionary Ecology* **19:** 467–486.

Low M. 2005. Female resistance and male force: context and patterns of copulation in the New Zealand stitchbird *Notiomystis cinta*. *Jounal of Avian Biology* **36:** 436–448.

McComb K, Clutton-Brock T. 1994. Is mate choice or aggression responsible for skewed distributions of females on leks? *Proceedings of the Royal Society of London Series B, Biological Sciences* **255:** 13–19.

McKinney F, Evarts S. 1997. Sexual coercion in waterfowl and other birds. *Ornithological Monographs* **49:** 163–195.

Mateos C. 1998. Sexual selection in the ring-necked pheasant: a review. *Ethology, Ecology and Evolution* **10:** 313–332.

Mateos C, Carranza J. 1995. Female choice on morphological features of male ring-necked pheasant. *Animal Behaviour* **49:** 737–748.

Mateos C, Carranza J. 1996. On the intersexual sexual slection for spurs in the ring-necked pheasant. *Behavioral Ecology* **7:** 362–369.

Matyjasiak P, Jablonski PG, Ollejniczak I, Boniecki PI, Lee SD. 1999. Foraging cost of a long tail ornament : an experiment with sand martin females. *Ethology* **105:** 521–530.

Mesnick SL, LeBoeuf BJ. 1991. Sexual behaviour of male northern elephant seals: 2. Female response to potentially injurious encounters. *Behaviour* **117:** 262–280.

Møller AP, Hedenstrom A. 1999. Comparative evidence for costs of secondary sexual characters : adaptive vane emargination of ornamented feathers in birds. *Journal of Evolutionary Biology* **12:** 296–305.

Møller AP, Nielsen JT. 1997. Differential predation cost of a secondary sexual character: sparrowhawk predation on barn swallows. *Animal Behaviour* **54:** 1545–1551.

Møller AP, Thornhill R. 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour* **55:** 1507–1515.

Nefdt RJC. 1995. Disruptions of matings, harassment and lek-breeding in Kafue lechwe antelope. *Animal Behaviour* **49:** 419–429.

Ophir AG, Persaud KN, Galef BG. 2005. Avoidance of relatively aggressive male Japanese quail (*Coturnix japonica*) by sexually experienced conspecific females. *Journal of Comparative Psychology* **119:** 3–7.

Pandit SA, van Schaik CP. 2003. A model for leveling coalitions among male primates: toward a theory of egalitarianism. *Behavioral Ecology and Sociobiology* **55:** 161–168.

Paul A. 2002. Sexual selection and mate choice. *International Journal of Primatology* **23:** 877–904.

Persaud KN, Galef BG. 2005a. Eggs of female Japanese quail are more likely to be fertilized by a male that she prefers. *Journal of Comparative Psychology* **119:** 251–256.

Persaud KN, Galef BG. 2005b. Female Japanese quail (*Coturnix japonica*) mated with males that harass them are unlikely to lay fertilized eggs. *Journal of Comparative Psychology* **119:** 440–446.

Plavcan JM, van Schaik CP. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology* **103:** 37–68.

Promislow DEL, Montgomerie R, Martin T. 1992. Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society of London Series B, Biological Sciences* **250:** 143–150.

Reale D, Bousses P, Chapuis JL. 1996. Female-biased mortality induced by male sexual harassment in a feral sheep population. *Canadian Journal of Zoology – Revue Canadienne de Zoologie* **74:** 1812–1818.

Rubenstein DI. 1986. Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW, eds. *Ecological aspects of social evolution*. Princeton, NJ: Princeton University Press, 282–302.

Safina C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. *Oikos* **43:** 159–164.

Scribner KT, Smith MH. 1990. Genetic variability and antler development. In: Bubenik GA, Bubenik AB, eds. *Horns, proghorns and antlers*. New York, NY: Springer-Verlag, 460–473.

Scribner KT, Smith MH, Jones PE. 1989. Environmental and genetic components of antler growth in white-tailed deer. *Journal of Mammalogy* **70:** 284–291.

Shine R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* **33:** 269–277.

Shine R, Mason RT. 2005. Does large body size in males evolve to facilitate forcible insemination? A study on Garter snakes. *Evolution* **59:** 2426–2432.

Smith SM. 1982. Raptor 'reverse' dimorphism revisited: a new hypothesis. *Oikos* **39:** 118–122.

Smuts BB, Smuts RW. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals; evidence and theoretical implications. *Advances in the Study of Behavior* **22:** 1–63.

Van Schaik CP, Hodges JK, Nunn CL. 2000. Paternity confusion and the ovarian cycles of female primates. In: van Schaik CP, Janson CH, eds. *Infanticide by males and its implications*. Cambridge: Cambridge University Press, 361–387.

Van Schaik CP, Pandit SA, Vogel ER. 2005. Toward a general model for male–male coalitions in primate groups. In: Kappeler P, van Schaik CP, eds. *Cooperation in primates and humans*. Berlin: Springer Verlag, 151–171.

Von Schantz T, Göransson G, Andersson G, Froberg I, Grahn M, Helgee A, Wittzell H. 1989. Female choice selects for a viability-based male trait in pheasants. *Nature* **337:** 166–169.

Von Schantz T, Grahn M, Göransson G. 1994. Intersexual selection and reproductive success in the pheasant *Phasianus colchicus*. *American Naturalist* **144:** 510–527.

Walther BA, Clayton DH. 2005. Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps. *Behavioral Ecology* **16:** 89–95.

Westneat D. 1987. Extra-pair copulations in a predominantly monogamous bird: observations of behaviour. *Animal Behaviour* **35:** 865–876.