Female Choice in Birds and the Cost of Long Tails

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EXPERIMENTAL AND OBSERVATIONAL STUDIES suggest that many extravagant and seemingly costly secondary sexual characters have evolved in response to sexual selection through female choice[1]. It has proved more difficult, however, for researchers to agree on the selective forces involved in the evolution of female mating preferences, especially when there is no direct fitness benefit for choosy females[2]. There has also been a lack of consensus as to the types of evidence that will distinguish between the three main solutions – runaway and good-gene models that invoke indirect selection, and sensory exploitation models that invoke direct

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selection[3]. For fieldworkers, the problem, when stripped to its essence, is that all three models are compatible with a present-day relationship between trait size and male quality.

Recently there have been renewed attempts to solve the problem. First, Møller suggested that females use asymmetry in secondary sexual characters to determine male quality[4], and has now shown that female barn swallows (*Hirundo rustica*) prefer males with symmetric tails[5]. Fluctuating asymmetry reflects the susceptibility of an individual to environmental and genetic stress, with increased asymmetry in stressed individuals[5]. Measurements of museum skins indicate that, within species, males with longer tails have more symmetric tails[6] (but see Ref. 7). So tail length may reliably reflect male

quality as predicted by good-gene models. However, the negative correlation between tail length and asymmetry could also be a byproduct of runaway. That is, only relatively viable males may be capable of producing fully grown tails, which are also more symmetric because of these males' viability. The female preference for symmetric tails is more convincing evidence for good-gene processes, but it could also be due to sensory exploitation because of a general sensory bias in animals toward symmetric shapes[8].

Second, Enquist and Arak have used computer neural networks to model the evolution of female preferences for long-tailed conspecifics[9]. Their results strongly suggest that all recognition systems contain 'hidden' female preferences. However, while knowledge of sensory biases provides information about the likely direction of the evolution of preferences, it does not preclude a role for indirect selection in their subsequent elaboration[3]. The problem of discriminating between the different models appears insoluble.

The latest attempt to resolve the impasse merits consideration because of its innovative approach. In a new paper in *Nature*, Balmford *et al.*[10] have used a comparative analysis and aerodynamic theory to investigate the costs of tail elongation for different species of bird. The analysis is based on a recent model of lifting surfaces by Thomas[11] which applies classic aerodynamic studies of airplane wings[12] to the lift and drag associated with birds' tails. The model suggests that the aerodynamically optimal tail shape is triangular when spread, hence forked when closed. Those parts of the tail posterior to the triangle do not increase the lift generated, and merely add to the drag. The amount of drag increases as the proportion of the total tail area distal to the triangle is enlarged.

If the basic tail is one with all feathers of equal length, resembling a fan, four derived tail types can be identified: (1) graduated tails, where all the feathers increased in length, except for the outer feathers which remained unchanged; (2) pintails, where only the central feathers increased in length; (3) shallow-fork tails, where the outer feathers increase in length so that the tail is approximately triangular when spread; and (4) deep-fork tails, where the outer feathers project far beyond the optimal triangular shape when the tail is spread. Modelling shows that the aerodynamic costs of elongating a tail vary depending on which feathers are enlarged. The cost analysed by Balmford *et al.* is the drag:lift ratio of the spread tail at a constant angle of attack. Graduated tails incur the greatest cost per unit length increase. In contrast, pintail elongation is far less costly, because a smaller proportion of the tail is distal to the optimal triangle. Forked tails are actually less costly than a simple tail with equal length feathers! Only when the outer feathers project beyond a triangle (a deep-fork tail in the closed state) do the flight costs rise.

Balmford *et al.* used these theoretical results to test several predictions about the selection costs imposed by different tails. They measured over 600 museum skins, ensuring in all cases that phylogenetic effects were controlled for, before making comparisons[10]. The following four predictions were tested:

(1) If sexual selection is less important in the evolution of forked tails than in that of graduated tails or pintails, there should be less sexual dimorphism in tail length in fork-tailed species. Pairwise comparisons of nine pairs of closely related species supported this prediction.

(2) Deep-fork tails are more costly than shallow-fork tails, hence more likely to be due to sexual selection. A pairwise comparison of eight pairs of fork-tailed species showed that species with deep forks are more sexually dimorphic in tail length, suggesting a greater role for sexual selection.

(3) Streamer tails (pintails and deep forks) are less costly per unit length increase than graduated tails, so there should be an association between tail length and tail type. In a phylogenetically controlled test, the relative tail length of species with streamers was greater than that of species with graduated tails.

(4) Species that are highly reliant on flight should have less costly tails. In those families that spend a lot of time in flight (or that migrate) there are fewer species with graduated tails, and more with streamers, than in families that are more terrestrial (or that do not migrate).

The close fit between predictions and results shows that natural selection, in the form of flight costs, plays a far more important role than previously recognized in determining the phylogenetic distribution of tail type and length. Species which rely heavily on flight are far less likely to have aerodynamically costly tails. In some ways this result is unsurprising as natural selection continues to operate, no matter what the strength of sexual selection. What was less obvious prior to this study, however, was the extent to which natural selection could account for variation in the kind of tails males possess, as well as their relative length.

Aerodynamic modelling provides a cautionary tale – when it comes to the costs of producing a long tail, some tails are less of a handicap than others. Tails that appear 'unimpressive' to our eyes, such as fan-shaped tails with feathers of equal length, are actually more aerodynamically costly than forked tails, even those with spectacular outer feathers ten times longer than the central feathers[10]. (Of course, the frame of reference is important. For example, a transition from a shallow- to a deep-forked tail increases aerodynamic costs and may therefore result from sexual selection.) Clearly, more care is needed before concluding that a long tail imposes a large cost. In fact, there are only a handful of empirical studies showing that tail elongation imposes substantial flight costs on birds[13-15]. Changes in wing morphology, for example, may greatly reduce the costs of a suboptimal tail type[14].

There are, of course, additional costs associated with elongated tails. Physiological and nutritional costs may be associated with the production of longer feathers, especially when these are brightly coloured. There are also more subtle costs associated with different kinds of tails. The risk of damage may be a particularly important factor because tail asymmetry, through either damage or natural variation in growth, is more costly for certain tail types. For example, a high proportion of the total lift in a forked tail is generated by the outer tail feathers. Asymmetry in these feathers will thus have a much larger effect on flight costs, by increasing rolling and yawing forces, than in a tail with feathers of equal length[16]. In general, as the distance between the tip of an outer feather and the midline of a bird increases, the drag force rises. Hence the turning force induced by asymmetry increases as outer tail feathers grow away from the midline of the bird[17]. Experimental work on barn swallows has confirmed that tail asymmetry decreases manoeuvrability[18].

Natural selection is clearly an underacknowledged force shaping birds' tails, but can aerodynamic analysis tell us anything about the role of sexual selection in tail elongation? Balmford *et al.*'s results provide evidence of a link between the strength of sexual selection and tail type[10]. In species with tails that have a small aerodynamic cost, such as forked tails, there is less sexual dimorphism in tail length. They suggest that this demonstrates reduced levels of sexual selection associated with these tail types. However, there is an alternative explanation. Their results also show that species with streamer-type tails tend to be more aerial, so even a small deviation from the optimum tail length under natural selection may be very costly for males. Sexual dimorphism reflects the net effect of the opposing forces of sexual and natural selection. Because natural selection is likely to be stronger in fork-tailed (aerial) species, decreased dimorphism does not necessarily reflect lower levels of sexual selection. A more detailed analysis in which the role of natural selection is incorporated into the predictions about sexual dimorphism will probably yield a more robust conclusion.

Does aerodynamic analysis allow us to distinguish between Fisherian and good-gene processes? Balmford *et al.* make the novel suggestion that the initial costs of elongating different feathers provide a clue to the reliability of different tail types as honest signals of male quality[10]. They emphasize that this approach is probably limited to families in which flight is less important. Forked tails are unlikely to have evolved as honest signals of male quality because, in the initial stages of feather elongation, they actually improve flight efficiency. Graduated tails result in the greatest cost per unit length increase. They are the tail type most likely to reflect a male's ability to incur a handicap, and hence to have evolved by good-gene processes. Pintails and deep-fork tails are less likely to have evolved through good-gene processes, because their evolution involves relatively low cost feather elongation, and may best be accounted for by Fisherian runaway. So, when looking at closely related species with similar flight behaviour and mating systems, they suggest that tail elongation in the species with a graduated tail is more likely to reflect good-gene processes than is tail elongation in the species with a pintail or a forked tail.

An alternative view is that any deviation from the optimal tail shape, irrespective of tail type, imposes a cost and may thus reflect good-gene processes. To paraphrase Gertrude Stein, a cost is a cost is a cost. Even so, the question still remains: which costs are honest signals? Further comparative and experimental studies will provide some fascinating answers.

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Can Animals Be Spiteful?

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LOGIC SUGGESTS that when members of a species interact with each other at least nine kinds of consequence are possible, because both actors and recipients may benefit (+), suffer (–) or experience no effect (0) (Box 1). When both the actor and the recipient benefit from an interaction (+,+), it is termed cooperation; this is widespread in the living world. When the actor benefits and the recipient suffers (+,–), the interaction is termed selfishness, which is even more abundant in the living world. When the actor suffers while the recipient benefits (–,+), the interaction is termed altruism. Compared to cooperation and selfishness, altruism is less common; nevertheless there are many examples of it in the animal kingdom. Altruism is not so easy to explain as cooperation or selfishness, but much has been learnt about its evolution in the last 25 years.

We now understand two mechanisms by which altruistic behaviour

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can evolve. Hamilton's rule[1], which states that the benefit to the recipient devalued by the genetic relatedness between actor and recipient should be greater than the cost to the actor, specifies a set of precise conditions for the evolution of altruism. An alternate mechanism for the evolution of altruism, pointed out by Trivers, is reciprocity[2,3]: if altruistic behaviours performed by an individual are reciprocated at some future time, such altruism may be favoured by natural selection.

What all of this means, of course, is that there is no real altruism and that all behaviour is really selfish in the long run or at the genetic level. But there is no doubt that the apparent paradox associated with altruism was largely responsible for the attention this behaviour has received and for the consequent revolutionary changes in the study of animal behaviour[4–6].

If both the actor and the recipient suffer as a result of an interaction (–,–), it is called spite. Conventional wisdom has it that to be spiteful is the prerogative of humans alone. It is true that there is no unequivocal example of interaction between animals where both actor and recipient clearly suffer. With no clear-cut real-life examples known, theoreticians have not been too active in this area. Puzzled by the absence of good examples of spite in natural populations, Hamilton[7] (1970) suggested a softening of our definition so that 'behaviour which harms others without benefit to the self may well be called spiteful'. More detailed investigations of examples of potential spite, even by this softened definition, are likely to enhance our understanding of the evolution of animal behaviour greatly, much as altruism has done in the past and continues to do so today.

At least two clear-cut examples of such 'weak spite' (see Box 1) have been demonstrated in the animal kingdom. The first came from a study of the western gull *Larus occidentalis* and the herring gull, *L. argentatus* in Newfoundland, Canada, a decade ago[8–10]. The gulls showed two kinds of behaviours that probably represent weak spite and have been interpreted as such by Pierotti[8,10]. The first behaviour, called piracy or kleptoparasitism, was directed at conspecific neighbours rather than to members of other species (as is usually the case