Testing the functional significance of tail streamers

MATTHEW R. EVANS AND A. L. R. THOMAS*

Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK

SUMMARY

Studies of the evolution of elaborate ornaments have concentrated on their role in increasing attractiveness to mates. The classic examples of such sexually selected structures are the elongated tails of some bird species. Elongated tails can be divided into three categories – graduated tails, pin tails and streamers. There seems to be little debate about whether graduated and pin tails are ornaments; i.e. costly signals used in mate choice. However, in the case of streamers there is considerable discussion about their function. It has been suggested that tail streamers could be (i) entirely naturally selected, (ii) entirely sexually selected, (iii) partly naturally and partly sexually selected. The prime example of a species with tail streamers is the swallow (*Hirundo rustica*) in which both sexes have tail streamers. In this paper we discuss the aerodynamic consequences of different types of manipulation of the streamer and/or outer tail feather. We make qualitative predictions about the aerodynamic performance of swallows with manipulated tail streamers; these predictions differ depending on whether streamers have a naturally or sexually selected function. We demonstrate that these hypotheses can only be separated if tail streamers are shortened and changes in aerodynamic performance measured during turning flight.

1. INTRODUCTION

Sexual selection is thought to have been important in the evolution of many apparently costly ornaments such as the antlers of deer and the patches of colour found in a variety of birds and fish. However, the classic examples of sexually selected structures are the elongated tails of birds (Andersson 1994). Experimental manipulation of the length of the tail ornaments of many birds have confirmed Darwin's (1871) suggestion that these ornaments play a role in mate choice; males with artificially elongated tail ornaments are more attractive, whereas males with shortened tail ornaments are less attractive (Andersson 1982; Møller 1988; Andersson 1992). The benefits of the possession of the ornament are clear and apparently uncontroversial. The problem which remains is why all individuals do not produce ornaments of maximum size. All theoretical mechanisms for sexual selection predict that ornaments will be costly at stable equilibrium (Fisher 1930; Lande 1980; Grafen 1990; Pomiankowski *et al.* 1991). It is this cost which maintains the honesty of the signalling system.

Tail ornaments can be divided into three categories (Balmford *et al.* 1993) – graduated tails e.g. long-tailed widowbirds (*Euplectes progne*), pin tails e.g. sunbirds (*Nectarinia spp.*) and streamer tails e.g. swallows (*Hirundo rustica*). There is apparently little debate about the first two categories. Theoretical analyses and empirical studies (Evans & Hatchwell 1992; Evans & Thomas 1992; Balmford *et al.* 1993) support the view

that both graduated tails and pin tails are costly at all levels of elongation. However, there is still discussion over the function of tail streamers (Møller 1988, 1989, 1994; Norberg 1994).

In experiments in which swallows were made to fly through a maze, which necessitated frequent abrupt changes in flight direction (Møller 1991), males with naturally long tails performed better than males with shorter tails. However, as tail length was not manipulated this experiment did not directly demonstrate that the swallow's tail streamers are costly. A recent aerodynamic analysis (Norberg 1994) suggested that the swallow's tail streamers may function as a control device, automatically adjusting the leading edge of the tail to form a vortex flap (Lee & Ho 1990; Thomas 1993*a*) when the tail is raised or lowered; this would increase lift and reduce drag.

Most of the lift on the tail is generated by the leading edges – which are formed by the outermost tail feathers. It has been known for some time that if the leading edges of a delta wing are drooped, the lift acting on the leading edges is increased, and the drag is reduced (Lee & Ho 1990; Thomas 1993*a*). Swept winged aircraft employ vortex flaps that can be deflected when extra lift is required (during landings or tight turns, for example). Norberg (1994) has suggested that the tail streamers of the swallow are automatic control devices that deflect the leading edges of the tail to form a vortex flap whenever the tail is lowered to generate lift. The mechanism is subtle. The shaft of the outer tail feather has a gentle rearwards curve, and this curve continues into the streamer. Therefore the centre of area of the streamer lies behind the torsional axis of the feather insertion. When the tail is lowered, the drag

* Current address: EGI, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

Figure 1. The manipulation performed on the outer tail feathers and the appearance of swallow tails following manipulations of outer tail feather length through basal manipulation. All tails are drawn to scale (Møller 1994) and assume a manipulation of ± 20 mm.

of the streamer, acting behind the torsion axis, rotates the outer tail feather and droops the leading edge of the tail. The system must be carefully tuned so that there is an appropriate level of torsional stiffness in the feather insertion to match the curvature of the feather shaft and area of the tail streamer (Norberg 1994). With the correct tuning of these three parameters the

tail streamer will act to automatically give the leading edges of the tail the correct droop for any given angle of attack (unlike the vortex flaps of aircraft which can be either deflected, or not). The potential advantage of the system is large: the vortex flaps of aircraft can increase the lift to drag ratio of the tail by over 30% and reduce drag by about 20% (whereas the streamers

Figure 2. Minimum turning circles of male swallows when (*a*) outer tail feathers are manipulated at the base of the feather but the Norberg mechanism still operates; (*b*) outer tail feathers are manipulated at the base of the feather but the Norberg mechanism is destroyed by the manipulation; (*c*) outer tail feathers are manipulated by changing the size of the streamer; (*d*) tail streamers removed entirely. Calculations assume a ± 20 mm manipulation. Minimum turning circles are calculated following Thomas (1993*b*), the Norberg mechanism is assumed to produce a 30% increase in tail lift as shown by Norberg & Thomas (unpublished). For all figures the inner circle illustrates the performance of an unmanipulated male, for (*a*), (*b*) and (*c*) the outer circle is the male with shortened tail and the intermediate circle in (*b*) is the male with the elongated tail. The swallow outline is to scale with the turning circles.

increase the drag of the tail by a small fraction of one percent even when the tail is furred).

Norberg's mechanism suggests that the swallow's tail streamers could have evolved via natural selection alone. In swallows both sexes possess tail streamers which could be used to support the view that the streamer is wholly or partially naturally selected. The discussion can be broken into two related questions:

1. Are the tail streamers of female swallows naturally or sexually selected structures? Møller (1994) suggests that female streamer length may reflect female quality; females with longer tails were more likely to lay a second clutch, fed their chicks at a higher rate and had higher reproductive success than females with shorter tails. However, Norberg's (1994) hypothesis suggests that the tail streamers of female swallows could be

naturally selected aids to flight. In contrast to both these functional explanations, Cuervo *et al.* (1996) suggests that female swallows may only have streamers because of a genetically correlated response to their possession by male swallows. Cuervo *et al.* (1996) also present data which demonstrates that females with longer tails do not have higher reproductive success than females with short tails; this apparently contradicts the findings of Møller (1994).

2. Are the tail streamers of male swallows naturally or sexually selected structures or has sexual selection acted on a pre-existing naturally selected streamer to make it even longer?

There are three testable hypotheses:

- (1) tail streamers are the product of sexual selection, the difference in length between the streamers of males

and females representing different optima in the two sexes. Different optima would be expected because of the differential costs and benefits of advertisement to mates by the two sexes;

(2) tail streamers are naturally selected for aerodynamic function, the difference in length between the streamers of males and females representing different optima in the two sexes. Different optima would be expected because the two sexes differ in wing shape and other morphological parameters (Møller 1994) and also differ in some ecological parameters e.g. the amount of incubation carried out;

(3) the tail streamers of female swallows are naturally selected and the difference in length between male and female streamer length is the sexually selected portion.

Swallows have been the focus of one of the most successful series of field investigations of sexual selection (see Møller 1994). Experiments and observations since 1988 have demonstrated that females preferentially mate with males with elongated outer tail feathers (Møller 1988; Smith & Montgomerie 1991), that males suffer a cost to tail elongation (Møller 1989) and that the length of the outer tail feather is influenced by parasite load and environmental conditions (see Møller 1994 for review). The experiments of Møller and co-workers have used a manipulation technique which changes the length of the outer tail feather by adding or subtracting 20 mm from the basal portion of the tail, producing tails having the appearance shown in figure 1 (Møller 1988, 1989, 1994; H. Smith, J. Aparacio personal communication). One consequence of this form of manipulation is that while outer tail feather length is changed streamer length remains unaltered.

The Norberg mechanism (Norberg 1994) explains the evolution of a streamer and depends on the ability of the tail feather to flex to produce lift when the tail is spread and lowered. In order to test the hypothesis that the streamer is a naturally selected structure the length of the streamer must be manipulated. Therefore, the work of Møller and co-workers cannot falsify the Norberg mechanism (as streamer length in these experiments remains unchanged) and so sheds no light on whether the streamer has evolved via natural or sexual selection.

The objectives of this paper are two-fold:

1. To investigate the aerodynamic consequences of the different ways of manipulating the outer tail feathers of birds with forked tails.

2. To make predictions which will allow the three hypotheses for the evolution of tail streamers to be tested.

Changing the length of a tail feather will result in changes in aerodynamic performance (Evans & Thomas 1992). We have calculated the minimum turning circles which could be achieved by birds with different manipulations of outer tail feather length (figure 2). Turning performance depends on the maximum lift coefficient a bird can generate. During a steady turn lift not only balances weight but must also provide a turning force. During turns swallows use their tails to generate lift in addition to that generated by the wings (Thomas 1993*b*). We have used a

technique which calculates the contribution of the tail to turning performance by combining the lift and drag of the tail with Pennycuik's model of bird flight (Pennycuik 1968, 1975, 1989). This approach can predict the minimum effect of ornaments on performance during steady turns (Thomas 1993*b*). We have modelled the effects of two different forms of manipulation of the outer tail feather of a forked tailed bird.

2. AERODYNAMIC CONSEQUENCES OF MANIPULATIONS AT THE BASE OF THE OUTER TAIL FEATHER

Figure 2*a* demonstrates that when the length of the outer tail feather is altered by changing the length of the basal part of the feather both tail feather elongations and reductions result in increased minimum turning circles.

Birds in which the outer tail feather is elongated experience an increase in drag due to the increased amount of tail feather. This is small as drag changes in proportion to the product of the width of added feather and the square root of its length both of which are small compared to the rest of the bird's body. This increase in drag results in a small increase in the minimum turning circle (*ca.* 2%); this is only marginally visible in figure 2*a* as the change in turn radius is similar to the line thickness.

Birds in which the outer tail feather is shortened experience a marginal reduction in drag (outer tail feather reduced in size). This change in drag is overwhelmed by a reduction in lift due to the change in the maximum continuous span of the tail (Thomas 1993*a*). The net effect is a relatively large increase in the minimum turning circle (*ca.* 10%).

These predictions assume that changing the length of the outer tail feather in this manner does not prevent the Norberg mechanism from operating. As the Norberg mechanism relies on the subtle relations between the stiffness of the feather, its curvature and area, it is possible that changing the shape of the tail feather in this way could destroy the tuning of the feather and stop the Norberg mechanism operating. If this is the case the streamer becomes no more than a drag producing structure equivalent to a ribbon attached to the tail. The predictions in this case would be that birds given elongated tails show a much larger minimum turning circle than unmanipulated birds and birds given shortened tails will have larger minimum turn radii than birds with elongated tails as they also suffer a reduction in lift for the reasons stated above (figure 2*b*).

Manipulations of outer tail feather length have produced changes in the attractiveness of males etc. (see Møller 1994). The effects outlined above are purely aerodynamic and how they map onto behavioural variables will depend on ecological factors, e.g. foraging technique, and will depend on the relative importance of flight in different behaviours. These predictions of changes on specific aspects of flight performance cannot be applied directly to behavioural measures.

3. AERODYNAMIC CONSEQUENCES OF MANIPULATIONS OF THE STREAMER

Figure 2*c* demonstrates that changing the length of the streamer part of the tail feather produces much smaller changes in turning performance than changing outer tail feather length. The lift produced by the Norberg mechanism will decrease following streamer manipulations as the tuning of the streamer is changed. Shortening streamers will have a small effect on the drag produced by the tail but this will be overwhelmed by the reduction in lift produced by the Norberg mechanism. Figure 2*d* illustrates an extreme case when the tail streamer is removed completely and hence the Norberg mechanism is destroyed. This extreme manipulation produces similar changes in minimum turn radii to those produced by manipulations of the outer tail feather through basal manipulation (cf. figure 2*a,b*).

It is clear that the different manipulations are likely to produce different aerodynamic effects. The predictions made here are based purely on the mechanical and aerodynamic consequences of the manipulations and tell us nothing about the way in which the streamer may have evolved. The following discussion is concerned with making more detailed, testable predictions from the sexual selection, natural selection and

partial sexual and partial selection hypotheses. As the Norberg mechanism is concerned with the evolution of a streamer, it is appropriate to manipulate streamer length and not outer tail feather length. The following discussion assumes that such a manipulation is made.

4. DISCRIMINATING BETWEEN HYPOTHESES FOR THE EVOLUTION OF STREAMERS

Naturally selected structures are predicted to be at an optimum level which maximizes the net benefit of the trait. If the streamer is at a naturally selected optimum then deviations away from this optimum should increase costs, i.e. both elongations and shortening should increase flight costs. Figure 3*a* shows the trajectory of costs against streamer length for both male and female swallows. For convenience we have considered that both sexes pay the same amount for their optimum streamer length.

All theoretical mechanisms for sexual selection predict that ornaments will be costly at stable equilibrium (Fisher 1930; Lande 1980; Grafen 1990; Pomiankowski *et al.* 1991). Therefore, if the streamer is the product of sexual selection it should be a costly trait and the cost should rise as streamer length is increased and should drop as streamer length is reduced. Figure

Figure 3. Relation between streamer length as it is manipulated away from the observed length and costs of tail streamers in male and female swallows. (a) Streamers in both male and female swallows are the product of natural selection with different optima for the two sexes. (b) Streamers in both male and female swallows are the product of sexual selection. (c) Streamers in male swallows are produced by a natural selection with increases beyond the naturally selected optimum being produced by sexual selection; female swallows have naturally selected streamers. (d) Illustration of how the three hypotheses can be discriminated, when streamer length is increased all hypotheses predict an increase in costs. If streamer length is reduced the natural selection hypothesis predicts an increase in costs, sexual selection predicts a decrease in costs and the combined natural and sexual selection hypothesis predicts a decline followed by an increase.

Figure 4. Illustrative surfaces showing the relation between the costs of turns with different curvature and streamer length for three different situations. (a) The way in which the costs would be expected to change if the Norberg mechanism operates. Straight flight costs continuously increase at a slow rate with streamer length; for turning flight there is some optimal streamer length which minimize costs. (b) The way in which costs would be expected to change if the streamer is entirely sexually selected and has no aerodynamic function – costs always continuously rise. The point where the tail moves from the furled position to the unfurled position is given by the x on each graph. This illustrates the importance of measuring more than one aspect of flight performance. For example, it would be impossible to distinguish between the natural and sexual selection hypotheses if only level flight costs were assessed (plane given when curvature = 0); it is only possible to distinguish these hypotheses in turning flight.

3b shows the trajectory of costs against streamer length for both male and female swallows if their streamers are purely the products of sexual selection. An optimum tail length will be produced in both sexes through the interaction of this cost function with a putative benefit function in which mating success increases with streamer length.

A more complicated situation arises if the streamer is the result of both natural and sexual selection. In figure 3c we have assumed that the female streamer length is optimal and that increases beyond this are produced by sexual selecting operating on the male. The cost function for females is the same as in figure 3a but in males costs increase with streamer length after this optimum has been passed. The observed male tail length will be some way up this increasing part of the

function—the increased cost being balanced by the mating advantages of increased tail length.

As can be seen in figure 3d the three hypotheses for the evolution of streamers can be separated by tracking the change in costs as streamers are manipulated down from the observed streamer length. The natural selection hypothesis predicts a continuous increase in costs, the sexual selection hypothesis predicts a continuous decline in costs while the combined sexual and natural selection hypothesis predicts an initial drop in costs followed by a rise. Increases in streamer length are predicted to increase costs under all hypotheses.

So far we have considered the impact of tail streamer manipulations on flight performance in a general fashion. However, the Norberg mechanism will only operate in turning flight and not in level flight (Norberg 1994). This means that in level flight all hypotheses predict that flight costs will increase with streamer length due to the change in drag produced by the furled tail. Figure 4 illustrates how costs should change with flight curvature and streamer length. Observations and theory (Thomas 1997) suggest that tails are spread abruptly as soon as flight begins to turn. This produces a step in the cost function. If the tail is the product of natural selection then the Norberg mechanism can operate from the point the tail is spread, this will act to produce a minimum in the cost function during turning flight. If the tail streamer is the product of sexual selection, then no minimum exists, and costs increase continuously with both streamer length and turn curvature.

This analysis demonstrates that the three hypotheses for the evolution of streamers can only be separated in turning flight and when streamers are reduced in length.

We thank David Bryant, Peter Hudson, Thaís Martins and Louise Rowe for discussions and constructive criticism. Henrik Smith and José Arevalo provided details of the ways in which they manipulated swallows tails. Three anonymous referees commented on an earlier version of the manuscript. This work was funded by a Natural Environment Research Council grant to M.R.E.

REFERENCES

- Andersson, M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature Lond.* **299**, 818–820.
- Andersson, M. 1994 *Sexual selection*. Princeton: Princeton University Press.
- Andersson, S. 1992 Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. *Anim. Behav.* **43**, 379–388.
- Balmford, A., Thomas, A. L. R. & Jones, I. L. 1993 Aerodynamics and the evolution of long tails in birds. *Nature, Lond.* **361**, 628–630.
- Cuervo, J. J., de Lope, F. & Møller, A. P. 1996 The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behav. Ecol.* **7**, 132–136.
- Darwin, C. 1871 *The descent of Man, and selection in relation to sex*. London: Murray.
- Evans, M. R. & Hatchwell, B. J. 1992 An experimental study of adornment in the scarlet tufted malachite sunbird. II. The role of the elongated tail in mate choice and experimental evidence for a handicap. *Behav. Ecol. Sociobiol.* **29**, 421–427.

- Evans, M. R. & Thomas, A. L. R. 1992 The aerodynamic and mechanical consequences of elongated tails in the scarlet tufted malachite sunbird: measuring the cost of a handicap. *Anim. Behav.* **43**, 337–347.
- Fisher, R. 1930 *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Grafen, A. 1990 Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* **144**, 473–516.
- Lande, R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305.
- Lee, M. & Ho, C. M. 1990 Lift force of delta wings. *Appl. Mech. Rev.* **43**, 209–221.
- Møller, A. P. 1988 Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature, Lond.* **332**, 640–642.
- Møller, A. P. 1989 Viability costs of male tail ornaments in a swallow. *Nature, Lond.* **339**, 132–135.
- Møller, A. P. 1991 Sexual ornament size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond. B* **243**, 59–62.
- Møller, A. P. 1994 *Sexual selection and the barn swallow*. Oxford University Press.
- Norberg, R. Å. 1994 Swallow tail-streamer a mechanical device for self deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc. R. Soc. Lond. B* **257**, 227–223.
- Pennycuik, C. J. 1968 A wind tunnel study of gliding flight in the pigeon *Columba livia*. *J. Exp. Biol.* **49**, 509–526.
- Pennycuik, C. J. 1975 Mechanics of flight. In *Avian biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp. 1–75. New York: Academic Press.
- Pennycuik, C. J. 1989 *Bird flight performance: a practical calculation manual*. Oxford University Press.
- Pomiankowski, A., Iwasa, Y. & Nee, S. 1991 The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* **45**, 1422–1430.
- Smith, H. G. & Montgomerie, R. 1991 Sexual selection and tail ornaments of North American barn swallows. *Behav. Ecol. & Sociobiol.* **28**, 195–201.
- Thomas, A. L. R. 1993a On the aerodynamics of birds' tails. *Phil. Trans. R. Soc. Lond. B* **340**, 361–380.
- Thomas, A. L. R. 1993b The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond. B* **254**, 181–189.
- Thomas, A. L. R. 1997 The flight of birds that have wings and tails: variable geometry expands the envelope of flight performance. *J. Theor. Biol.* (In the press.)

Received 19 August 1996; accepted 30 September 1996