

COMMENTARIES

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Foraging Cost of Ornaments Which Are Not Ornaments: Comment on Matyjasik et al. (1999)

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Cuervo, J. J. 2000: Foraging cost of ornaments which are not ornaments: comment on Matyjasik et al. (1999). Ethology 106, 659—663.

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In a recent article Matyjasik et al. (1999) tested the hypothesis that the cost of a long forked tail ornament can be due to impaired foraging. The authors lengthened, experimentally, the outermost tail feathers of female sand martins (*Riparia riparia*) and checked the flight cost of the manipulation in terms of foraging cost, i.e. feeding rates and prey items size. They found that tail-elongated females decreased the rate at which they fed nestlings, and that they captured more but smaller insects. These results would indicate the foraging cost of a tail ornament in the sand martin and would be consistent with the expectations of the handicap model of sexual selection. Similar experiments by Møller and collaborators in the barn swallow (*Hirundo rustica*) have shown that experimental elongation of tail length in males has a detrimental effect on feeding rates and insect prey quality (Møller 1989; de Lope & Møller 1993; Møller & de Lope 1994; Møller et al. 1995). The authors argue that the results of the barn swallow studies might be biased because the apparent detrimental effect of elongated tails in males could be due to a decrease in male parental effort in response to an increase in female parental effort. Female change in behaviour might be a consequence of increased male attractiveness (differential allocation of female parental effort; Burley 1986). Matyjasik et al. (1999) solved this problem, because female sand martins do not increase their attractiveness by possessing longer tail feathers.

First of all, I agree that the results from the barn swallow experiments were not confounded by the differential allocation of female parental effort. Møller and collaborators did not assess foraging costs of tail length manipulation in terms of male feeding rates, but exclusively by measuring the size of prey items. (Møller 1989; Møller & de Lope 1994; Møller et al. 1995). In de Lope & Møller (1993)

feeding rates were also included because differential allocation of female parental effort was being tested. The assumption that the differential allocation of female parental effort does not affect the size of prey items captured by males is based on the studies by Turner (1982) of optimal foraging by swallows. The capture of a large insect item requires the expenditure of more energy than the capture of a small insect item, mainly because large insects fly faster than small insects. However, these high flight costs are exceeded by the high caloric value of large insects. The net energy gained from a prey item (energy of prey item minus energy cost of capture) is 32.9 calories for large prey, but it is only 5.3 calories for a small item (Turner 1982). In other words, large insects are more profitable than small ones. As a response to a perceived increase in female parental effort, male swallows would presumably work less, i.e. they would supply less food to the nestlings. However, independently of the amount of food that males supply to the young, males should try to maximise their net energy gain. This maximisation cannot be achieved by changing to smaller prey items, because, as I have shown above, feeding on small insects is less profitable than feeding on large insects.

However, even though optimization is an unlikely explanation, the change in prey size to smaller prey items after experimental tail elongation is not necessarily a consequence of impaired flight due to tail manipulation. Neither Møller and collaborators nor Matyjasik et al. realized that other explanations are possible. Maximization of the rate of energy intake is an optimal strategy only if feeding behaviour does not entail other costs, such as predation risk. If experimental elongation of tail feathers increased predation risk, for instance by making swallows or martins more conspicuous to predators, individuals should minimize all foraging costs (including predation risk), even at a cost of profitability. Cost minimization in feeding strategies has been found already in a fish species (Milinski & Heller 1978). The aim of the paper by Matyjasik et al. (1999) was to test whether sexual ornaments impose viability costs upon their bearers. However, it is clearly stated by Matyjasik et al. that outermost tail feathers of female sand martins are not sexual ornaments. It is obvious that in order to test the cost of flight of an ornament, the trait to be experimentally manipulated has to be an ornament. Matyjasik et al. have tried to imitate, in female sand martins, the ornamental outermost tail feathers of male barn swallows. However, the cost of flight of an individual with experimentally elongated, non-ornamental tail feathers in one species is not comparable to that of an individual of another species with ornamental tail feathers, partly because ecological, behavioural, and life history traits differ among species. Additionally, the cost of secondary sexual characters can be reduced by the presence of cost-reducing traits (Møller 1996). For birds with ornamental tails, elongation and enlargement of wings and narrowing of the outermost tail feathers have been demonstrated to act as cost-reducing traits (Andersson & Andersson 1994; Balmford et al. 1994). Therefore, the resultant shape of a non-ornamented species after the experimental lengthening of tail feathers is not comparable with the shape of another species with naturally elongated tails. The acquisition of an ornamental feather is not simply the elongation of an ordinary feather. The whole morphology and physiology of an organism may change during the evolution of such a character elongation (Møller 1996).

According to aerodynamic models, a forked tail with outermost tail feathers twice as long as central tail feathers closely approaches the aerodynamic optimum shape (Thomas & Balmford 1995). An increase in tail length exceeding the optimum ratio of 2 should increase the cost of flight (Thomas 1993; Evans & Thomas 1997). On the other hand, Norberg (1994) has suggested that long tail streamers in swallows might have an aerodynamic function by improving manoeuvrability. However, naturally selected structures are predicted to be at an optimum level that maximises the net benefit of the trait, and whatever the current tail length is, any further experimental elongation will displace tail length beyond its optimum and will thus be energetically costly. Moreover, when outermost tail feathers are ornaments, sexual selection also has some influences on the shape of the tail. Mating preferences for long tails generate longer tail feathers than the optimum according to aerodynamics, and this should increase the cost of flight. Any further experimental elongation of ornamental tails will produce an extra increase in the cost of flight. Therefore, independently of the hypothesis that explains the evolution of outermost tail feathers, its experimental elongation will always be followed by an increase in the cost of flight. Consequently, in order to test the cost of ornamental tail feathers, it is necessary to shorten those feathers. Only if we detect a decrease in the cost of flight as a result of the experimental shortening can we conclude that sexual selection has made the feathers evolve beyond their optimum length according to natural selection, and that they hence induce a cost. Obviously, if tail shortening is too exaggerated, it may give rise to a feather shorter than the optimum according to natural selection, and we might also find an increase in the cost of flight. The importance of shortening as an alternative to elongation of tail feathers in order to test hypotheses of their functions and the relative importance of different selection forces has been emphasised already (Evans & Thomas 1997; Thomas & Rowe 1997).

According to Matyjasik et al. (1999), the handicap model of sexual selection predicts that elaborate ornaments impose viability costs upon the bearers. The authors pretend to have shown the foraging cost of a tail ornament in the sand martin, and they conclude that their findings are consistent with the handicap principle. However, both the handicap model (Zahavi 1975; Andersson 1986; Heywood 1989; Grafen 1990; Iwasa et al. 1991) and the Fisherian model (Fisher 1930; Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991) of sexual selection predict that ornaments will be costly at the stable equilibrium. The distinctive prediction of the handicap hypothesis, shared with no other model of sexual selection, consists of ornaments being more costly to low-quality than to high-quality individuals (see references of the handicap model above). It might be possible to test whether the differential costs to high- and low-quality signalers exist if we could identify those individuals *a priori*. We would expect high-quality individuals to be less affected by a given manipulation than low-quality individuals. Even if the authors had succeeded in demonstrating foraging costs as a result of tail ornamentation, this finding would equally support the handicap or the Fisher hypothesis.

Additionally, there are two minor objections to Matyjasik et al. (1999) that

deserve to be mentioned. Firstly, the authors have manipulated tail length in female sand martins because they believe that outermost tail feathers in females are not the targets of male selection and, hence, they have controlled for the possible effect of differential allocation of parental effort. However, they could also have manipulated tail length in males, since outermost tail feathers in sand martins are not ornamental feathers in either sex. Secondly, tail length had been manipulated by 2 cm in all previous barn swallow studies. In the case of the barn swallows with the shortest outermost tail feathers (females from southern populations), this manipulation implied 24% of the total feather length (Cuervo et al. 1996a, b). Matyjasik et al. (1999) have also manipulated tail length by 2 cm, but for sand martins this implies 36% of tail length. It is not surprising then that such a dramatic change in tail length had an effect on foraging costs. Evans & Thomas (1997) and Thomas & Rowe (1997) had pointed out already that such a massive experimental change in feather length is inappropriate when studying the function of elongated tail feathers.

It was indeed a good idea to investigate the relationship between length of ornamental tail feathers and feeding rates to the young, since this particular indicator of foraging cost could not be used in the experiments by Møller and collaborators with the barn swallow. However, Matyjasik et al. (1999) is clearly a flawed attempt because they should have manipulated the length of ornamental feathers, or feathers longer than the optimum according to natural selection, and tail feathers in sand martins are not ornamental feathers.

Acknowledgements

A. P. Møller, M. Taborsky and A. Thomas made helpful comments on the manuscript. I was supported by Spanish DGICYT (PB95-0110).

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Received: July 12, 1999

Initial acceptance: January 12, 2000

Final acceptance: February 10, 2000 (M. Taborsky)