

large to be removed efficiently in diffusive-controlled processes¹³.

Of course, the mass loading values obtained with a simple first-order model can only be used to make order of magnitude judgements and it is not justifiable to assert that smelting activities at Norilsk are responsible for Arctic haze in Alaska. The numbers and back trajectories do suggest, however, that air emissions associated with combined industrial activity in central Eurasia may constitute a so far undetermined, but seemingly significant, portion of Arctic haze observed in the American Arctic.

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Female choice selects for extreme tail length in a widowbird

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Darwin's¹ hypothesis that male secondary sexual ornaments evolve through female preferences is theoretically plausible^{2–7}, but there is little experimental field evidence that such preferences exist^{8–10}. I have studied female choice in relation to male tail length in the long-tailed widowbird, *Euplectes progne*, and report here that males in which the tail was experimentally elongated showed higher mating success than males having normal or reduced tails. The possibility that intrasexual competition among males maintains the long tail was not supported: males with shortened tails held their territories as long as did other males. These results suggest that the extreme tail length in male long-tailed widowbirds is maintained by female mating preferences.

Male long-tailed widows have the most extreme sexual ornaments among *Euplectes*, an African genus of polygynous weaverbirds (the Ploceidae)¹¹. Reproductive adult males are black except for a red epaulet on the wing, but the most conspicuous feature is the tail: 6–8 of the 12 tail feathers are ~0.5 m long, the rest being one- to two-thirds as long. The tail during flight display is expanded vertically into a deep, long keel below the male as he flies with slow wingbeats 0.5–2 m above the territory. Displaying long-tailed widows are visible from over 1 km distance on their 0.5–3-hectare territories. The territories lie in open grassland on the Kinangop plateau, Kenya, where *E. progne* is one of the most common birds, and where the present study was performed between November 1981 and March 1982. Females are inconspicuous, being mottled brown, with short tails (~7 cm). They build their nests on the territories of the males, in the upper third of the 0.5–0.8 m-high grass, *Eleusine jaegeri*, and raise their young (2–3) unaided by the male. These features make the long-tailed widow

suitable for a test of the theory of intersexual selection of male ornaments.

Darwin¹ and Fisher² suggested that further evolution of an ornament ceases when it becomes so large that it reduces survival enough to exactly balance the mating advantage. For this to be so, females must prefer larger than normal-sized ornaments; otherwise there can be no balance between the two selection pressures. In the present experiment, females chose from males with shortened, normal or elongated tails. The Darwin–Fisher theory therefore predicts that mating success should be highest among males with elongated tails, and lowest among males with shortened tails.

The experiment included nine groups, each containing four individually colour-ringed males, of similar initial tail length and territory quality. Territory boundaries were determined by plotting on maps the locations of male displays and attacks, using cattle fences, streams and vegetation features as landmarks. In each matched group, the following treatments were randomly allocated among the four males. The tail was cut to ~14 cm in one of them; each removed feather was then attached with rapidly (~1 s) hardening cyanoacrylate glue to the corresponding feather in another male, whose tail was thus prolonged by an average of 25 cm. About 3 cm of each removed feather was first cut off and glued back on to its counterpart in the 'shortened' male, which hence was manipulated in a similar manner to the 'elongated' male. The two remaining males were controls; one was ringed only. To check whether the cut-and-glue operation influenced male behaviour or female choice, the tail of the second control male was cut off at the midpoint; each feather was then glued back on again. This operation shortened the tail by only 1 cm (~2%), which is probably not noticeable by females. Uneven joints or ends of glued feathers were trimmed with a scalpel. The joints were difficult to see from more than 1 m.

As capture and manipulation might influence subsequent behaviour, which could confound interpretation, flight displays and territorial disputes were counted in each male for 30 min 1–5 days before, and 10–14 days after the treatment.

Male mating success was estimated by the number of active nests (containing eggs or young) on each territory, for which I searched for about 1 h just after treatment of the male, and at weekly intervals for 1 month afterwards. No new clutches were laid after early January. To avoid bias, I searched each territory in proportion to its area of nesting habitat (tall, rank grass). The first count provided a standard with which to compare male mating success after tail treatment, estimated by the number of clutches laid during the remainder of the breeding season, after the day on which the male was manipulated. This use of each male as his own control reduces the importance of differences in territory quality, which influences female choice of mate in the long-tailed widow (*M.A.*, in preparation). Counts spanned 1 month, so a few nests might represent re-laying, but this should not bias the result as treatments were randomized within each group.

Euplectes females usually seem to mate with the male on whose territory they nest^{12,13}. The possibility that a female might mate with one male and nest on the territory of another should not produce bias favouring the Darwin–Fisher prediction but should reduce the likelihood of detecting female mating preferences in the present study. Whereas attractive males in such cases receive more matings, some of their females may build on the less crowded territories of less attractive males. Group defence against nest predators is poorly developed, and there is no other evidence that female long-tailed widows would benefit from clumped breeding; the nests are well dispersed within a territory.

Females will be selected to respond to a character only if it varies among potential mates¹⁰. This is the case in long-tailed widows: the fully grown tails (no blood quills) of seven territorial males had a mean length of 49.6 cm, with c.v. = 9.4%. There was no significant correlation between male tail length and number of nests on the territory before the experiment.

However, the present randomized block design is unsuitable for detecting such a correlation; it was used to make the experiment maximally sensitive to any importance of tail length.

The two types of control males (I, cut and restored; II, only ringed—see Fig. 1) did not differ significantly in tail length, display rate or any other measured character. Therefore, they should be equivalent from a female perspective, so I have treated them as one category below, with two representatives in each group of four males.

Before tail treatments, there were only minor differences in mating success between 'shortened', control and 'elongated' males (Fig. 1a). After treatment, however, mating success changed as predicted by the female choice hypothesis, with lowest success for males having shortened tails, and highest

success for males with elongated tails (Fig. 1b). Hence, tail length apparently did influence mate choice: females preferred those males having the longest tails. As the main difference was between 'elongated' males and other males (including controls), the difference did not result from possible destruction of species-specific features in males having shortened tails.

Another possible explanation is that 'shortened' males became less active in their courtship behaviour, or that males with elongated tails became more active. However, the only indication of a difference was the reverse of this (but not significant: $P > 0.95$, Friedman two-way analysis of variance). Males having reduced tails increased their average rate of flight display slightly (from 9.2 to 10.3 displays per 30 min), whereas control males showed a decrease (from 10.3 to 6.9), as did males with elongated tails (from 10.8 to 7.8). Therefore, changes in male behaviour were probably not responsible for the higher success of elongated males.

In choosing her mate, a female should respond to the quality of his territory, on which she nests^{10,14}. However, due to the randomization within each group of four males and the use of each male as his own control, territory differences cannot explain the higher mating success of males with elongated tails. As behavioural differences were also excluded, I conclude that the changes in male tail length caused the differences in the attraction for females.

As is implicit in the Darwin-Fisher theory of sexual selection, females preferred males having tails that were longer than normal. This is expected if females are attracted by 'supernormal stimuli'^{4,6,8}. Such a preference can evolve if asymmetrical selection shapes female responsiveness^{4,15}. One possibility is that a male's sexual ornaments reflect his overall phenotypic and genotypic quality, so that females choosing highly ornamented males bear offspring having high expected fitness⁹. However, it is unknown whether fitness in nature is heritable enough to influence female choice of mate.

Highly adorned males can be favoured by active mate choice, where females compare males before accepting one, but also by easier detection¹⁶. This latter advantage may have contributed to the evolution of the long tail and the flight display in the long-tailed widow. The lateral surface of the displaying male is enlarged 2-3 times by the tail, making him correspondingly easier to discover from a distance in the open habitat. However, neighbouring males often display simultaneously, and females sometimes visit several males in rapid succession with ample opportunity for comparisons. The long tail is therefore probably maintained at least partly through active female discrimination among males.

Alternatively, ornaments may be favoured by intrasexual selection among males competing for territories or hierarchy ranks^{9,10,17}. This hypothesis predicts that males having shortened tails are least efficient at holding a territory, and that males with elongated tails are most efficient; this was not supported. Most males remained on their territories until February, when the nesting was over, and territory tenacity did not differ among treatment categories ($P > 0.6$, Pitman randomization test). There was no evidence of increased territory size in males having elongated tails. Males with shortened tails took off and defended their territories more often than other males but the difference was not significant ($P > 0.1$, Friedman two-way analysis of variance); this may indicate more intrusions on their territories. However, 'shortened' males also increased their rate of flight display (see above), usually performed when the male is alone on the territory, or is visited by females. Easier flight in these males relieved of the unwieldy tail, which is carried only during the breeding season, may explain their higher rate of territory defence as well as flight display (insofar as the non-significant differences are real).

The results presented here support Darwin's¹ hypothesis that certain male ornaments are favoured by female mate choice, and probably evolved through it.

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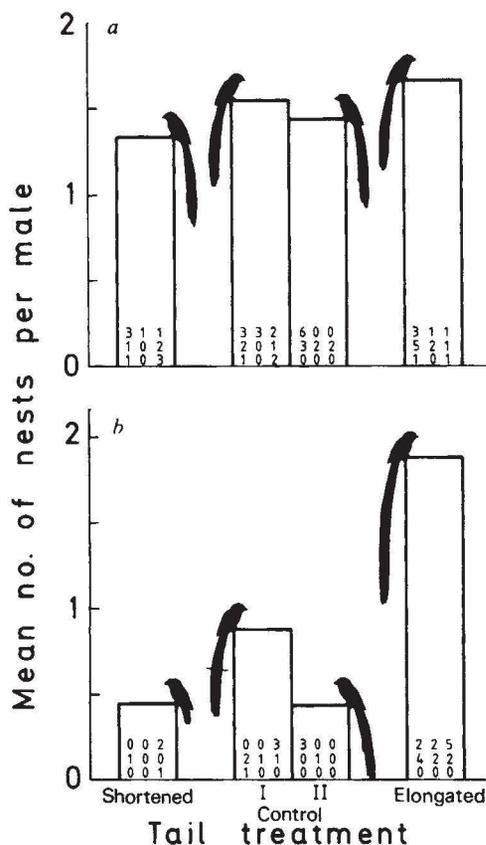


Fig. 1 Mating success in male long-tailed widows subjected to different tail treatments. *a*, Mean number of active nests per territory for the nine males of the four treatment categories, before the experiment. Numbers of nests for the nine males in each of the four categories are given at the bottom of the bars, always in the same order of matched 4-group. *b*, Number of new active nests in each territory after treatment of males. The following procedure was used to test for differences in mating success between the treatment categories. For each male I calculated the difference between the number of new active nests on his territory during the remainder of the breeding season after tail treatment, and the original number of nests on the territory before tail treatment. (Subtraction of the original number of nests reduces the influence of initial variation among males and territories.) These differences were used for matched comparisons (with respect to each group of four males) between shortened, control and elongated males. As predicted by the Darwin-Fisher theory of sexual selection, males with elongated tails became significantly more successful (as measured above, compared with before the tail treatment) than shortened males and control males II ($P < 0.05$ in both cases, paired randomization tests). For the four categories tested together, there was a significant trend of increasing mating success as tail length increased from shortened via control to elongated males ($P = 0.03$, Pitman randomization test¹⁸ adapted to the present experimental design; no standard test fits this situation, with two different treatments (shortened and prolonged tails) and two control categories, and an alternative hypothesis which predicts a specified trend).

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Self-pituitary grafts are not rejected by frogs deprived of their pituitary anlagen as embryos

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In the present study, we have adopted the model of Triplett¹ to reinvestigate the timing of development of immunological tolerance to self-organ-specific antigens. We have removed pituitary or eye² anlagen from frog embryos before development of the immune system and returned them at a later time as differentiated organ implants to their now immunocompetent larval or adult original owners. If immunological tolerance to these putative organ-specific self-antigens occurs at an early and fixed time period, then organ-deprived hosts, lacking the opportunity to become tolerant, would be expected to reject such implants¹. Our results show that self-implants were never rejected whereas control allogeneic implants were usually rejected by larval hosts and were always rejected by adult hosts. These data, which contrast with those reported by Triplett, suggest that frogs, and perhaps other higher vertebrates, can become tolerant to self-organ-specific antigens throughout life.

We recently reported² experiments in which eye anlagen were removed from *Rana pipiens* and *Xenopus laevis* (*X. laevis* and *X. laevis-gilli* hybrid clones³) embryos. When the enucleated embryos developed into immunocompetent larvae, they were implanted with either their own (previously parked) or an isogenic (cloned) differentiated eye. All self-grafts in intact hosts or enucleated hosts survived in almost perfect condition for as long as they were observed (>100 days; Fig. 3a, b). In contrast, allogeneic eyes were rejected by about half of the intact larval *Xenopus* and *Rana* hosts.

Because only some of the larval hosts rejected allogeneic eyes², and because other studies had demonstrated a greater degree of tolerance of skin allografts in larval than adult hosts⁴, we enucleated cloned (LG15) *Xenopus* embryos (Nieuwkoop and Faber⁵ stages 26–32) and implanted them with an isogenic eye 2 months after they metamorphosed. In such postmetamorphic *Xenopus*, all allogeneic eye implants were rejected vigorously and rapidly (most within 20 days), whereas isogenic implants on intact or embryonically enucleated hosts survived for as long as they were observed (2–24 months, Figs 1, 3c). Examination of serially sectioned isogenic implants fixed at

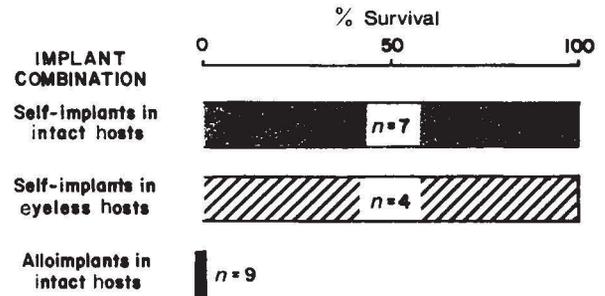


Fig. 1 Per cent survival of self- (▨) and allogeneic (■) eye implants in intact postmetamorphic *Xenopus* and of self-implants in embryonically enucleated postmetamorphic *Xenopus* (▧) at 90 days post-implantation. The number of frogs in each group is indicated within the bars. All enucleations were performed during stage 26–32. One animal, however, developed a partial regenerated eye that was re-extirpated at about stage 43.

1–2 yr post-implantation revealed no lymphocytic infiltration or other evidence of immune destruction.

To minimize the criticism that the eye may not be a good model organ to study development of unresponsiveness to organ-specific antigens and to determine the generality of our observations with the eye, we used the pituitary as a test organ. Triplett reported that most (10/13) self-pituitary implants were rejected by their embryonically hypophysectomized larval tree frog hosts with a mean graft survival time of ~40 days. This study suggested that the pituitary has organ-specific transplantation antigens, and provided experimental support for the idea that unresponsiveness to these antigens must develop in a fixed early time period relative to lymphocyte ontogeny. In our studies, pituitary anlagen were extirpated from Shumway⁶ stage 17–18 *R. pipiens* embryos and 'parked' orthotopically on previously hypophysectomized stage 17–18 sibling hosts. After 50–60 days, we dissected the now differentiated pituitaries free from the brain of the 'parking' host and implanted them in the dorsal tail-fins of the original hosts. The hypophysectomized hosts were pale and their growth was retarded (Fig. 3d). After implantation of either a self- or an allogeneic pituitary, they began to darken due to melanophore stimulating hormone (MSH) release by the implanted gland, and their growth rate increased. Six of nine allogeneic pituitaries were rejected within 20 days. Recipients of these implants again became pale. In marked contrast, all recipients of the self-pituitaries remained dark for as long as they were observed (three for >90 days, Figs 2, 3e). Examination of serially sectioned heads of the hypophysectomized hosts showed no identifiable anterior pituitary cells in association with the brain of any of the six larvae examined (compare Fig. 3f and g). Thus, the darkening of pituitary implanted animals seemed to result from MSH production by the self-implant rather than from any anterior pituitary tissue remaining after embryonic ablation.

Three technical differences between our pituitary grafting experiments and those of Triplett may bear on our discordant observations. First, our experiments were done with *R. pipiens* while his were done with *Hyla regilla*. Thus, although the anlagen were extirpated at comparable stages of embryonic development, and the differentiated organs were reimplanted after about the same time lag, we cannot exclude the possibility that there are species-specific differences in the maturation of immunity and a narrower period in *Hyla* in which self-tolerance may occur.

A second experimental difference was the site in which the pituitary anlagen differentiated. In our experiments, the anlagen were 'parked' orthotopically in previously hypophysectomized age-matched sibling embryos. In contrast, Triplett 'parked' the anlagen under the ectoderm in the tail region in rather older nonsibling larvae¹. In this site, the graft induced formation of a heavily pigmented host-derived fibrous connective tissue capsule that was always transplanted together with the pituitary¹.