Experimental analyses of sexual and natural selection on short tails in a polygynous warbler

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We believe that no experimental study has yet tested Darwin's idea that, as well as generating trait elaboration, intersexual selection might sometimes drive sex-biased trait reduction. Here we present the results of two experiments exploring the negative relationship between tail length and reproductive success in male golden-headed cisticolas (*Cisticola exilis*). In the first experiment, artificially shortening a male's tail produced a dramatic increase in his reproductive success, measured as either the number of females nesting or number of chicks fledged on his territory. A second experiment, in which manipulated birds were flown through a maze, revealed that short tails also impose costs by reducing aerodynamic performance during slow-speed foraging flight. Because tail shortening yields reproductive benefits and viability costs, we conclude it has evolved via sexual selection. Disentangling exactly how short tails enhance male reproductive success is more difficult. Male–male competition appears partly responsible: aerodynamic theory predicts that tail reduction enhances high-speed flight and, in line with this, shortened-tail males spent more time engaged in high-speed aerial chases of rivals and defended higher-quality territories. However, shortened-tail males had higher reproductive success independent of territory quality and spent more time in aerial displays which may be directed at females. This suggests that tail shortening is also favoured via female choice based on male phenotype.

Keywords: short tails; tail manipulation; female choice; sexual selection; male–male competition; cisticola

1. INTRODUCTION

There is now widespread support for Darwin's (1871) idea that sexual selection can bring about sex-biased trait exaggeration (see Andersson 1994). Far less attention, both theoretical and empirical, has been paid to his corresponding suggestion (Darwin 1874) that sexual selection and, in particular, female mate choice could sometimes drive sex-biased trait reduction.

This omission is striking, especially given the potential importance of evidence of epigamic trait reduction in resolving competing models of sexual selection in situations such as leks, where mate choice is pronounced yet where choosy females appear to gain no direct benefits from their mating preferences. Indirect models of mate choice fall into two main groups (Kirkpatrick & Ryan 1991; Andersson 1994; Andersson & Iwasa 1996). According to good-genes models, the male traits preferred by females are consistently costly; provided there is heritable variation in quality, a male's ability to invest in such traits is thus an honest indicator to females of his ability to pass on good genes conferring high viability on her offspring. In contrast, under Fisherian models the degree of expression of preferred traits is heritable, but is not linked to heritable variation in male viability: hence, choosy females benefit by producing disproportionately attractive sons, but not more viable sons or daughters. While empiricists testing good-

genes models often assume that these predict that preferred traits should always be elaborate, models of the Fisher process explicitly predict that it can lead to either trait exaggeration or trait reduction (Lande 1981; Pomiankowski & Iwasa 1998). Hence, several authors have suggested that data showing that females consistently prefer less (rather than more) elaborate mating partners constitute strong support for Fisherian over good-genes models (Dawkins 1986; Cockburn 1991; Andersson 1994).

However, to date, evidence that intersexual selection can drive trait reduction is limited and equivocal (Ryan & Keddy-Hector 1992; Andersson 1994). In some swarm-forming dipterans, smaller males are more successful than larger males, probably because they are more agile and, hence, outcompete larger rivals in intrasexual contests over mates (McLachlan 1986; McLachlan & Allen 1987; Neems *et al.* 1990, 1992); the same may be true of Weddell seals (*Leptonychotes weddelli*) (Kooyman 1968; Riedman 1990). In moorhens (*Gallinula chloropus*) and mallards (*Anas platyrhynchos*), there is evidence that females prefer smaller mates (Petrie 1983; Holmberg *et al.* 1989). In *Drosophila subobscura*, such a preference apparently arises because smaller males are more agile and, hence, can dance more closely with females (Steele & Partridge 1988). Finally, in the polygynous dunlin (*Calidris alpina*), a reversal in sexual size dimorphism is associated with smaller males performing better aerial displays, which are apparently directed at females (Blomqvist *et al.* 1997): a finding which may shed light on similarly reversed size dimorphism in several other aerially displaying waders as well as bustards, manakins and hummingbirds (Payne

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1984; Jehl & Murray 1986). However, all of these studies are correlational, all deal with a general reduction in male body size, few have teased out female choice from male–male competition and none have provided strong evidence of female choice based on reduced male traits.

Against this background, a number of authors have cited the golden-headed cisticola (*Cisticola exilis*) as a species in which female choice has driven male trait reduction (Cockburn 1991; Andersson 1994; Hedenstrom 1995; Pomiankowski & Iwasa 1998). Hitherto, this claim was made largely because, despite being polygynous, this warbler exhibits an extraordinary reversal in sexual dimorphism, with males moulting before breeding to have far shorter tails (both absolutely and relative to body size) than breeding females (Lynes 1930; Cockburn 1991). The first ever field study on this species has now confirmed a very important element of this story by showing that male reproductive success (as measured by the number of females nesting on a male's territory) is consistently negatively correlated with male tail length (see Lewis *et al.* 2000). However, both the causality of the link between tail length and reproductive success and whether short tails are costly remain unresolved. Further understanding of this system requires an experimental approach.

This paper presents the results of two tail manipulation experiments on *C. exilis* aimed at tackling three issues. First, we wanted to confirm the direction of causality underpinning the link between tail length and male reproductive success and did so by manipulating the tails of 36 territory holders during the phase of territory establishment. Second, we conducted detailed observations on those birds and their territories in order to understand better the mechanisms by which tail length is important. Third, to be certain that tail reduction is sexually selected, we sought to exclude the possibility that, besides reproductive pay-offs, short tails also yield naturally selected benefits through enhanced flight performance. Eliminating this idea is important because conventional aerodynamic models predict that possessing a short tail reduces the cost of moderate- and high-speed flight (Thomas & Balmford 1995). However, while male cisticolas fly at these sorts of speeds during displays, they fly at far lower speed when foraging in dense vegetation. New aerodynamic theory, specific to very slow flight and confirmed by video analyses, suggests that, in this context, cisticolas use their tails as drag-based paddles to help them steer through reedbeds (A. L. R. Thomas, M. J. Lewis and A. Balmford, unpublished observations). Because drag increases with tail area, tail shortening may impose substantial costs by reducing the turning force generated by the tail and, hence, the rate at which slow-flying cisticolas can turn. We tested this final idea by assessing the aerodynamic performance of manipulated birds as they flew through a maze in which they were required to negotiate vertical strings that simulated dense vegetation.

2. METHODS

(a) Study area and study species

The experimental work presented here was conducted over two breeding seasons (1994–1995 and 1997–1998) as part of a

long-term study of *C. exilis* in 60 ha of grassland near Townsville in Queensland's wet–dry tropics (see also Lewis *et al.* 2000). The great majority of territorial males at the site and nearly all females nesting on their territories were individually known from colour bands.

Breeding at the site is limited to the wet season and starts with males establishing 0.2–1.4 ha territories in November and December. Territory holders advertise their presence by singing from prominent perches and exclude other males by vigorous aerial chases. They also perform lark-like aerial song displays that last up to 270 s and that are punctuated by as many as three steep dives to within 2 m of the ground; on all but the final dive of the display, the bird re-ascends either immediately (in which case we termed the behaviour simply a 'dive') or straight after an *ca.* 20 m zig-zag flight over his territory (termed a 'zig-zag dive').

Territory holders initiate nest construction by using spiders' webs to stitch living leaves together, but play no other part in parental care. Up to 14 females nest on a single male's territory, lining the nest shells with grass and laying clutches of one to five eggs. Most nesting occurs between early January and late March. Females produce as many as three clutches per season, but almost invariably switch territories between nesting events. Females usually forage away from the territory on which they are nesting. Further details of the social organization, reproductive behaviour and ecology of *C. exilis* are given elsewhere (Lewis *et al.* 2000).

(b) Field experiment

We tested the causality of the negative correlation between tail length and reproductive success of male *C. exilis* by manipulating (between November and early January) the tails of 36 males, which subsequently acquired territories on the study site. Males were caught in mist-nets, colour banded and measured (see Lewis *et al.* 2000) before being randomly assigned to one of four treatment types. Nine shortened-tail males had 4 mm sections excised from the basal part of their eight innermost tail feathers (under the upper tail coverts with cuts *ca.* 10 and 14 mm from the base); the proximal and distal portions were then rejoined using micropins inserted into the feather shafts and fixed with cyanoacrylate superglue. Using the same technique, the excised sections were inserted into the corresponding region of the tails of nine elongated-tail males. Nine control 1 males had their eight innermost tail feathers cut *ca.* 10 mm from the base and reglued without changing length (to control for the effects of gluing). Note that in all three manipulated groups, the two outermost feathers on each side of males' tails were unaltered. Finally, nine control 2 birds were kept for the same amount of time but released unmanipulated (to control for capture effects).

There were no differences across the treatment groups in wing length or natural tail length (ANOVAs across groups, on wing length $F_{3,32} = 0.81$ and n.s. and on pre-manipulation tail length $F_{3,32} = 1.27$ and n.s.). However, manipulation introduced significant variation in tail length (ANOVA, on post-manipulation tail length $F_{3,32} = 71.90$ and $p < 0.001$), decreasing and increasing the tails of shortened- and elongated-tail males, respectively, by *ca.* 2 s.d.s; the manipulated tail lengths (28.0–35.5 mm) lay within the natural range for breeding males (25.5–36.0 mm) ($n = 217$ males). By altering tail area, our manipulations changed tail drag (proportional to area); however, because *C. exilis* tails are graduated, lift generation (set by the length of the outermost feathers, which we did not change) was not affected by our treatments (for further explanation see Balmford *et al.* (1993) and Thomas & Balmford (1995)).

Figure 1. Schematic diagram of the maze used for assessing flight performance. Birds were released at the left-hand end and flew to the right. For clarity, the diagram depicts only half of the rows in the maze test section and only half of the strings in each row. The separation between rows was 20 cm and the separation between strings within rows decreased from 20 cm (at the left) to 5 cm (at the right). One video camera was aligned along the mean line of flight at the left-hand end and the second was aligned perpendicular to this at the same height and at the mid-point of the test section.

The reproductive success of our experimental males was monitored during daily censuses and measured in two ways—as the number of clutches initiated per territory (equivalent to the number of different females nesting on the territory) and as the total number of chicks surviving to day 10 (immediately prior to fledging). Molecular analyses of paternity are underway (P. Dunn, personal communication), but genetic paternity data are very unlikely to alter the present findings: given the very marked degree of social polygyny observed, those males with few females nesting on their territories would have to obtain exceptionally high numbers of extra-territory copulations with females nesting on more popular territories while suffering very low cuckoldry themselves to eliminate the patterns of pronounced reproductive skew observed. Moreover, *C. exilis* has extremely small testes for its body mass (M. J. Lewis, unpublished observations), indicating that promiscuous mating by females is uncommon (Møller 1991).

Each time a marked bird was seen during daily visits, its location was plotted on a 1:1250 map with the help of colour-coded stakes marking out a 25 m × 25 m grid. The area of each male's territory was measured as that of the minimum convex polygon (Southwood 1966) encompassing all of his song perches (defined in Lewis *et al.* 2000). We assessed the vegetation available in each territory during the peak of female nesting in two ways: as the height of the grass, and as the density of the favoured nesting plant *Sida* (expressed as the number of plants per square metre); both measures were made in five randomly placed 5 m × 5 m quadrats in each territory.

We obtained information about the behaviour of manipulated males through ten 15 min focal watches of each bird spread evenly through the female nesting period; all watches were conducted during the morning peak of activity (06.00–09.00 h). Time-budgets were monitored by one-zero sampling of all activities (every 15 s) and by continuous recording of all display flights, dives, zig-zag dives and aerial chases of males or females (Martin & Bateson 1986). The figures for the percentage of time males spent in different activities were arc-sine square-root transformed to achieve approximate normality (Sokal & Rohlf 1995).

(c) Maze experiment

We examined whether tail shortening was costly by flying another batch of manipulated males in breeding plumage through a maze in which, to escape the experimenter, they were required to negotiate vertical strings. These manipulations were simpler than those used in the field experiment. They involved exchanging the distal 12 mm of the eight innermost tail feathers of 12 males (who formed the shortened-tail group) with equivalent 9 mm sections cut from the tails of 12 other males (who formed the elongated-tail group); 12 control 1 males were treated as before, but this time there were no control 2 birds. The manipulations again introduced significant differences in tail length (ANOVAs, before manipulation, $F_{2,33} = 1.01$ and n.s., and after manipulation, $F_{2,33} = 90.61$ and $p < 0.001$; ranges of tail lengths, before manipulation, 28.9–32.5 mm, and after manipulation, 24.8–34.9 mm).

We quantified the impact of these manipulations on slow-speed flight by flying the birds through a maze 4 m long, 2 m wide and 1.5 m high containing 11 evenly spaced parallel panels of vertical strings, which decreased in separation from 20 cm down to 5 cm (figure 1). The maze simulated the dense vegetation through which cisticolas fly when foraging. Males were flown through the maze both immediately before and *ca.* 30 min after manipulation. Their flights were filmed using a pair of orthogonally mounted video cameras (filming at 50 fields s⁻¹) and the resulting tapes analysed to calculate the time taken to negotiate the maze and the number of strings hit *en route*. The sample sizes vary across treatment groups because not all birds flew through the maze on both occasions.

3. RESULTS AND DISCUSSION

(a) Impact of tail manipulation on male reproductive success

Males with artificially shortened tails had on average approximately two more clutches on their territories than control birds four more clutches than elongated-tail males (figure 2a) (ANOVA, $F_{3,32} = 6.66$ and $p < 0.01$; in

Figure 2. The impact of tail manipulations on the reproductive success of males measured as (a) the number of clutches and (b) the number of fledglings produced. The histograms show means $\pm$ s.e.s.

pairwise Tukey tests, shortened-tail males had significantly more clutches than all other groups of males at $p < 0.05$). When reproductive success was measured in terms of the numbers of chicks fledged, males with shortened tails were more than twice as successful as control birds and six times as successful as elongated-tail birds (figure 2b) (ANOVA on number of fledglings, $F_{3,32} = 8.35$ and $p < 0.001$; again, in Tukey tests shortened-tail males were more successful than all other groups of birds at $p < 0.05$). These results thus provide clear evidence that the link between tail shortening and male reproductive success is causal, but our field data coupled with aerodynamic theory also shed light on the mechanisms underpinning that link.

(b) Male-male competition or female choice?

In line with the results from correlational studies (Lewis *et al.* 2000), it seems likely that short tails are favoured in breeding males at least in part because they confer benefits in intrasexual competition over access to preferred territories. There were no differences in the size of the territories defended by males across the different treatment types (ANOVA comparing territory area across the four groups, $F_{3,32} = 0.36$ and n.s.). However, shortened-tail males defended territories that contained higher densities of *Sida* than those of any other group of males (figure 3a) (ANOVA comparing *Sida* densities, $F_{3,32} = 4.35$ and $p = 0.01$; in pairwise Tukey tests, shortened-tail males had higher *Sida* densities than the other groups at $p < 0.05$). The importance of tail length in determining territory quality was confirmed in a stepwise multiple

regression analysis in which no morphometric variable other than manipulated tail length of the holders predicted a significant amount of variation in *Sida* density on territories. This contrasts with results on unmanipulated birds in which both tail length and wing length were independently related to *Sida* density (Lewis *et al.* 2000); this difference might have arisen because our manipulations increased the variation in tail length to such a degree that it overwhelmed any effect of wing length. Manipulated tail length also affected the length of territory tenure: males with artificially elongated tails tended to hold territories for less time than other males, despite having been manipulated at the same stage of the season (figure 3b) (ANOVA comparing the length of territory tenure after manipulation, $F_{3,32} = 3.00$ and $p < 0.05$, with Tukey tests revealing that elongated-tail males abandoned their territories earlier than control 1 birds at $p < 0.05$; Julian dates of manipulation did not differ across treatments, $F_{3,32} = 0.53$ and n.s.).

We suggest that these results are probably explained by the impact of tail shortening on high-speed flight. According to conventional aerodynamic models (relevant at moderate to high flight speeds), possessing a short tail should decrease drag and thereby reduce the cost of high-speed flights such as male-male chases (Thomas & Balmford 1995). Consistent with these predictions, territory holders with shortened tails spent more time than other males chasing rivals out of their territories (figure 3c) (ANOVA on the percentage of time spent in male-male chases, $F_{3,32} = 7.19$ and $p < 0.001$; in Tukey tests, shortened-tail birds spent more time chasing males than the other groups of birds at $p < 0.05$). This could be because short tails enable males to spend more time defending favoured nesting areas, but could of course be interpreted as short-tailed males having to spend more time in territorial defence simply because their territories, by virtue of their high quality and/or greater attractiveness to females, are subject to higher rates of intrusions.

The aerodynamic prediction of tail shortening reducing the cost of high-speed flight should extend to display flights and dives, which are also performed at relatively high speeds. When we tested these predictions using our behavioural data, we found that our experimental males differed widely in the time spent in display flights and that elongated-tail males in particular displayed less often than other birds (figure 3d) (ANOVA on the percentage of time spent displaying, $F_{3,32} = 5.71$ and $p < 0.01$; Tukey pairwise comparisons were significant at $p < 0.05$ between elongated-tail and all other groups of birds). The treatments also affected dive and zig-zag dive behaviours, generally in the predicted direction (figure 3e) (ANOVA on the mean number of dives per watch, $F_{3,32} = 5.03$ and $p < 0.01$, with significant pairwise differences between elongated-tail and control 1 males and, more unexpectedly, between control 1 and control 2 males; ANOVA on the mean number of zig-zag dives per watch, $F_{3,32} = 3.48$ and $p < 0.05$, with elongated-tail birds performing fewer zig-zag dives than shortened-tail males at $p < 0.05$).

Unlike male-male chases, aerial displays, dives and zig-zag dives all peak well after territory establishment when females are choosing nest sites and copulating with males. They are thus unlikely to function primarily in male-male competition over territories and, while they

Figure 3. The impact of tail manipulations on male territoriality and display behaviour. (a) Shortened-tail males defended territories containing higher densities of *Sida*, the plant favoured by nesting females. (b) Elongated-tail males tended to abandon territory defence earlier. (c) Shortened-tail males spent more time in male-male chases. (d) Elongated-tail males spent less time in display flights. (e) Elongated-tail males executed fewer dives. The histograms show means $\pm$ s.e.s in all plots.

may still be intrasexual signals (involved, for instance, in mate guarding), they could equally well be directed at choosy females. Hence, short tails may be favoured by female choice directly—via choice for elaborate male displays—as well as indirectly—via choice for territories.

One final, equivocal piece of evidence suggesting that tail length might be favoured via female choice for male phenotype as well as via intrasexual competition comes from comparing how well male tail length and *Sida* density predicted the variation in male reproductive success. In bivariate regressions, manipulated tail length was better than *Sida* density at predicting variation in both the number of clutches and number of fledglings (for clutches, manipulated tail length yielded adjusted $r^2 = 0.40$, $n = 36$ and $p < 0.001$, and *Sida* density yielded adjusted $r^2 = 0.21$, $n = 36$ and $p < 0.01$; for fledglings, manipulated tail length yielded adjusted $r^2 = 0.37$, $n = 36$ and $p < 0.001$; *Sida* density yielded adjusted $r^2 = 0.16$, $n = 36$ and $p < 0.01$). These results were confirmed in multiple regressions. Manipulated tail lengths, *Sida* density and grass height on the territory, and wing length all independently predicted variation in the numbers of

clutches, but tail length was by far the strongest single predictor (see table 1 for the final model). When measured in terms of the number of young fledged instead, no variable predicted male reproductive success better than manipulated tail length and, after controlling for this, no additional predictor variables could be entered into the model (table 1).

Hence, the effect of tail length on male reproductive success cannot be entirely explained in terms of measured territory attributes. The tail manipulations altered male displays, which do not appear to be directly involved in territory defence. Moreover, after controlling statistically for variation in those aspects of territory quality which we quantified, shortened-tail males remained more successful. While this might be because we failed to measure an important aspect of territory quality, it seems more likely that female choice is based on male phenotype as well as territory quality.

(c) *The costliness of short tails*

While short tails yield reproductive benefits as a consequence of improved flight performance at high speeds

Table 1. Results of multiple regressions aimed at predicting variation in male reproductive success measured as the number of clutches or number of fledglings per territory

(For each model, $n = 36$ males.)

significant, independent predictors	number of clutches			number of fledglings		
	direction of effect	t	p	direction of effect	t	p
manipulated tail length	—	4.22	< 0.001	—	3.64	< 0.001
<i>Sida</i> density	+	2.10	< 0.05			
grass height	+	3.11	< 0.010			
wing length	+	2.42	< 0.05			
overall model		$r^2 = 0.58$	< 0.001		$r^2 = 0.37$	< 0.001

(probably via more than one route), the results of our maze experiment indicate that, during the kind of slow-speed flight adopted when foraging, tail shortening imposes substantial costs on breeding males. Looking first at the number of strings that birds hit in the maze, a repeated-measures ANOVA revealed no overall differences in the scores (averaged before and after manipulation) between treatment types or in scores (averaged across all treatment types) before versus after manipulation. However, there was a highly significant interaction between treatment type and whether the manipulation had yet been performed: hence, the manipulation had a strong effect which differed between groups (for the interaction, $F_{2,27} = 10.95$ and $p < 0.001$ and all other terms n.s.) (see figure 4a). To investigate how the effect of the manipulation varied, we then conducted pairwise t -tests, which showed that shortening increased and elongation decreased the number of strings that birds hit (for shortened-tail males, $t = 3.66$, $n = 11$ birds and $p < 0.01$, for control 1 males, $t = 0.92$, $n = 9$ and n.s., and for elongated-tail males, $t = 5.25$, $n = 10$ and $p < 0.001$).

Equivalent analyses on the times taken to fly through the maze ($\log_{10}$ -transformed to achieve approximate normality) again showed that the impact of manipulation varied across treatment types (repeated measures ANOVA yielded $F_{2,27} = 3.47$ and $p < 0.05$ for the interaction and all other terms n.s.) (figure 4b). This time, the only pronounced effect of manipulation was on shortened-tail birds (for shortened-tail males, $t = 2.22$, $n = 11$ and $p = 0.05$, for control 1 males, $t = 1.07$, $n = 9$ and n.s., and for elongated-tail males, $t = 1.52$, $n = 10$ and n.s.).

These differences in aerodynamic performance were not confounded by any variation in initial ability (comparing across groups prior to manipulation, ANOVA on number of strings hit, $F_{2,27} = 0.16$ and n.s., and ANOVA on $\log_{10}$ (time taken), $F_{2,27} = 0.34$ and n.s.). Because for ethical reasons we flew birds through the maze immediately after manipulation rather than holding them for a prolonged period, our measures may have underestimated the ability of birds to adjust to their new tail lengths. Nevertheless, elongation (as well as shortening) gave males novel tails (the former intermediate in length between summer and winter tails), yet elongated-tail males improved their flight performance (in terms of strings hit) immediately following manipulation. Hence, novelty effects alone cannot explain the impact of tail reduction on slow-speed flight; instead, it

Figure 4. The impact of tail manipulations on the aerodynamic performance of birds flying through the maze measured as (a) the number of strings hit and (b) the time taken. The histograms show means $\pm$ s.e.s. Significant pairwise differences before versus after manipulation at $p < 0.05$ are marked with asterisks.

appears that tail shortening *per se*, rather than manipulation in general, that is costly.

4. CONCLUDING REMARKS

The results presented here provide, as far as we know, the first experimental evidence that sexual selection can drive trait reduction. Male *C. exilis* with artificially shortened tails had more clutches laid and more chicks fledged on their territories than either control or elongated-tail males. These findings demonstrate that the consistent negative relationship between male tail length and reproductive success reported by Lewis *et al.* (2000) is driven directly by the effect of tail length rather than by correlations with another variable. Moreover, the maze

experiments show that, during foraging flight, possessing a short tail reduces aerodynamic performance and, thus, probably foraging efficiency. Tail shortening therefore bears the hallmarks of a classic sexually selected trait: it enhances male reproductive success, while at the same time imposing costs in a non-sexual context.

Teasing apart exactly why short tails are favoured is more difficult. As predicted by aerodynamic theory, tail shortening was associated with improved performance during high-speed flights. Shortened-tail males spent more time chasing other males and, associated with this, defended territories containing higher densities of the favoured nesting plant. This suggests that part of the reason for the success of short-tailed males is because they are more successful in intrasexual contests over access to high-quality territories.

However, in the field experiment (as among unmanipulated birds) (Lewis *et al.* 2000), male reproductive success also increased with decreasing tail length independently of variation in *Sida* density. This residual effect of tail length was associated with elongated-tail males performing fewer display flights, dives and zig-zag dives and has three possible explanations. These displays may enable males to obtain territories that are superior in ways that we did not measure (although this seems unlikely given that display rates peak well after territory establishment). Alternatively, these displays may be intrasexual signals involved, for instance, in mate guarding—with frequently displaying males having higher reproductive success either because they have more mates to guard or perhaps because females choose better guards to avoid harassment. Lastly, aerial displays may be the focus of direct female choice based on male phenotype (see also Lewis *et al.* 2000).

Clearly, further experiments are required in order to resolve fully how tail length affects male reproductive success. One approach would be to manipulate *Sida* density (or other territory attributes) rather than male tail length, while a second would be to manipulate male tail length after rather than during territory establishment and to see whether it alters male reproductive success in the absence of any changes in territory quality. These experiments are now underway.

Two other points are worth noting. First, even if these follow-up manipulations do show that tail shortening is partly driven by direct female choice based on male phenotype (rather than territory quality), this is probably because females prefer males with frequent or elaborate aerial displays (i.e. exaggerated traits) rather than short tails *per se* (i.e. reduced traits). Hence, we still lack experimental evidence for any species of a direct female preference for a reduced trait (Cockburn 1991; Ryan & Keddy-Hector 1992; cf. Darwin 1874; Andersson 1994; Hedenstrom 1995). Second, contrary to suggestions in the literature (Dawkins 1986; Cockburn 1991; Andersson 1994), even if it was shown that female *C. exilis* did prefer short tails themselves (and not the exaggerated displays which they facilitate), this would still not provide strong support for Fisherian over good-genes models of sexual selection. One reason is that we have not excluded the possibility that female cisticolas prefer short-tailed males in order to gain direct benefits such as avoidance of harassment. More importantly, our maze results show

that, like the long tails of many sexually selected birds (Balmford *et al.* 1993), short tails are aerodynamically expensive. They are therefore just as likely as long tails to reveal heritable variation in male quality and, hence, to have evolved via a good-genes process—which in turn raises the interesting question of why sexually selected trait reduction is so much rarer than trait enlargement (Ryan & Keddy-Hector 1992; Andersson 1994).

We thank Adam Felton, Sam Fox, Ashly and Carol Lewis, Beth Mott and Ian Owens for field assistance, Tim Birkhead, Jan Lindström and Phil Warren for help with the analyses and Malte Andersson, Tim Birkhead, Ben Hatchwell, Andrew Pomiankowski, Rufus Johnstone and three anonymous referees for comments on the manuscript. Permits for capture, banding and manipulation were kindly provided by the Australian Bird and Bat Banding Scheme, the Queensland Department of Environment and Heritage, the Royal Australian Air Force and James Cook University Ethics Committee. This work was financed by the Australian Research Council and the UK Natural Environment Research Council. A.L.R.T. is currently supported by a Royal Society University Research Fellowship.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.