

Forum

A novel evolutionary pattern of reversed sexual dimorphism in fairy wrens: implications for sexual selection

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Reversed sexual dimorphism (females being larger than males) occurs in several bird groups, including hawks and vultures (Accipitridae), falcons (Falconidae), sandpipers and snipe (Scolopacidae), phalaropes (Charadriidae), jacanas (Juncidae), skuas (Stercorariidae), boobies (Sulidae), frigate birds (Fregatidae), owls (Strigiformes), cuckoos (Cuculidae), hummingbirds (Trochilidae), manakins (Pipridae), and some ratites (Struthioniformes). In most cases, reversed sexual dimorphism (RSD) is present in many traits, and hence selection has been presumed to act non-independently on several characters (Lande and Arnold, 1983). Hence, RSD has commonly been discussed in terms of differences in body size (Mueller, 1990). In this study, we report a novel pattern of RSD in fairy wrens (Maluridae), which has important evolutionary implications for the ways in which sexual dimorphism can occur and the mechanisms of sexual selection.

We examined patterns of morphological sexual dimorphism, based on published data (Rowley and Russell, 1997; Schodde, 1982) and our own measurements (described later), within a molecular phylogeny for the Maluridae (Christidis and Schodde, 1997). This analysis revealed at least two independent occurrences of RSD in tail length (Figure 1). In one of these cases, the orange-crowned fairy wren *Clytomyias insignis*, the reversed dimorphism is associated with a small relative increase in tarsus and wing length in the female, as is commonly observed in species with RSD. However, reversed tail dimorphism in red-backed, white-shouldered and white-winged fairy wrens (*M. melanocephalus*, *M. alboscapulatus*, and *Malurus leucopterus*, respectively) is not associated with an increase in size of other female traits (Table 1). In the first two species, the male is larger in terms of tarsus and wing length, but the female has a significantly longer tail. Two island subspecies of the third species (*M. l. leucopterus* and *M. l. edouardi*) show the same pattern, but the mainland subspecies (which we have used as the designate species for the phylogeny) appears monomorphic in terms of tail length (*M. l. leuconotus*; Table 1). Although tail-length differences have previously been noted for fairy wren species (Schodde, 1982), the classification of RSD has not been formally described or quantitatively studied in any of these species. As far as we are aware, the RSD of a single trait (in an opposite direction to the body size dimorphism) is a novel pattern of evolution of tail elongation in birds. In a survey of published incidences of RSD, we could not find a single account that matched the morphological patterns observed in this cluster of three species of fairy wrens.

To explore whether this pattern of RSD in fairy wrens has arisen due to tail elongation in the female or tail shortening in the male, we examined changes in tail length, tarsus length, and wing length using the reduced squared-change parsimony algorithm in MacClade (Maddison and Maddison, 1992). In particular, we focused on the nodes preceding and including

those of the Malurus RSD complex (indicated as nodes 1 to 4 in Figure 1) to reconstruct the ancestral morphological states. Both tarsus and wing length (commonly interpreted as indicators of body size) decrease through the complex, with males remaining larger than females (Figure 2a, b). Changes in tail length show a very different pattern (Figure 2c). Initially (i.e., at node 1), males possess longer tails than females; but male tail length decreases at a faster rate than females, resulting in relatively longer tails in the females (nodes 1 to 3). When *M. alboscapulatus* branches off at node 3, tail length is further reduced, and the RSD is increased due to a larger reduction in tail length in the male. A slightly different pattern is observed as *M. melanocephalus* and *M. leucopterus* diverge at node 4. Male tail length is reduced further in *M. melanocephalus* and female tails are reduced only slightly (resulting in a large RSD), whereas overall tail length increases in *M. leucopterus*. The increase in tail length in *M. leucopterus* is shown to a greater extent in the males, resulting in sexual monomorphism (although two subspecies of *M. leucopterus* appear to regain tail length RSD).

Most hypotheses for the evolution of RSD have stressed the importance of sexual selection acting on increased female size (Mueller, 1990; Olsen and Cockburn, 1993) and simultaneous decreased male size (Amadon, 1975; Jehl and Murray, 1986; Lande, 1980; Mueller, 1990). We cannot invoke such hypotheses here, as there is no associated increase in female size in the species exhibiting RSD. Therefore, we need to consider alternative mechanisms by which the pattern of RSD could have arisen in these fairy wrens. There are no apparent systematic differences in mating system that could explain the differences in tail dimorphism across the species (Björklund, 1990; Schodde, 1982). Similarly, ecological specialization of these species appears to postdate the evolutionary trend for decreased male tail length (Schodde, 1982) and so cannot explain the observed dimorphism. The RSD species are also so obviously sexually dichromatic that it seems unlikely the tail length dimorphism could have evolved to reduce competition between mated pairs (or the sexes) for access to ecological resources such as food (Shine, 1989). We can also exclude hypotheses for RSD based on female ornamentation (Amundsen et al., 1997), as it appears that male tail length is decreasing rather than female tail length increasing.

We have generated three nonmutually exclusive hypotheses that could explain the observed pattern of RSD in fairy wrens. First, decreased male tail length could be a sexually selected ornament and could be used as a signaling device to discriminate among males (Jehl and Murray, 1986). Two of the species exhibiting RSD are known to exhibit unusually high levels of sexual promiscuity (approximately 50% of young are the result of an extrapair copulation in *M. melanocephalus*; Karubian J, unpublished data), allowing for high variance in male reproductive success and the opportunity for intense sexual selection (Webster et al., 1995). In each species, birds hold their tail in a cocked, upright position, which has led Schodde (1982) to describe the tail of fairy wrens as reflecting social position and displays involving the tail as being central to fairy wren social organization. Hence, it is possible that the morphology of the tail (in association with its movement) may be an important sexual signaling device. To test this hypothesis, one could perform mate choice and social dominance trials in which the length of males' tails is manipulated independent of other morphological and behavioral characters.

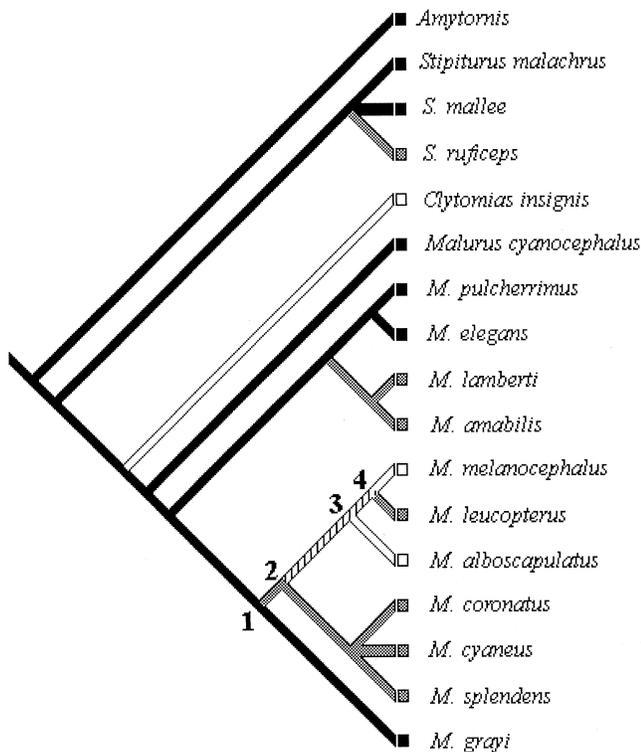


Figure 1
Strict consensus tree, based on allozyme data (Christidis and Schodde, 1997), indicating changes in sexual dimorphism in tail length in Maluridae. Dark lines indicate normal sexual dimorphism (i.e., males have larger tails than females); gray lines indicate sexual monomorphism; hollow lines indicate reversed sexual dimorphism (RSD; i.e., females have longer tails than males); striped lines represent an equivocal state between monomorphism and RSD. RSD has evolved on at least two separate occasions. The numbers 1 to 4 indicate nodes at which we reconstructed ancestral tail length by the reduced squared-change parsimony algorithm in MacClade (Maddison and Maddison, 1992).

Our second hypothesis predicts that decreased male tail length could render a mechanical advantage. These species of fairy wren possess graduated tails, which are thought to be aerodynamically costly ornaments when elongated (Thomas, 1993). Therefore, reduction of tail length could lead to increased flight performance and hence reduced predation risk, increased foraging efficiency, or lower flight costs for interterritory forays to seek extrapair copulations. The reduction in wing length observed across the clade (Figure 2b) may further increase flight costs and hence be an additional factor driving the reduction of tail elongation (Balmford et al., 1994). For this hypothesis to account for RSD, there would have to be differential flight costs associated with male and female behaviors and/or some partitioning of roles between the sexes in terms of flight behaviors (Lundberg, 1986). The influence of tail morphology on flight could be tested directly by tail length manipulations and controlled flight observations which include quantification of aerodynamic and biomechanical parameters to assess the flight costs of decreasing tail length (cf. Swaddle et al., 1999).

Finally, males and females may be subject to the same (directional) selection pressures acting on tail length, but the males have responded to a greater degree than females. This could occur if there was greater genetic variation in tail length in males but similar genetic variation in tarsus and wing length between the sexes (Shine, 1988). Genetic variation for

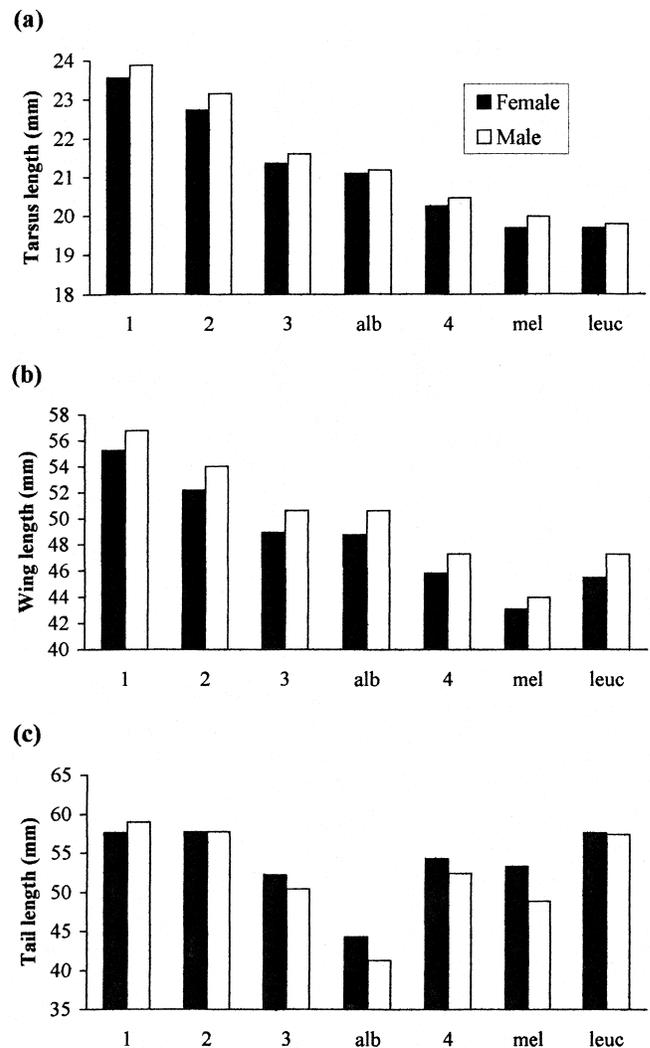


Figure 2
(a) Tarsus, (b) wing, and (c) tail length at phylogenetic stages preceding and within the *Malurus* reversed sexual dimorphism (RSD) complex of males (hollow bars) and females (filled bars). The numbers 1 to 4 refer to nodes 1 to 4 indicated on Figure 1; alb, *M. alboscapulatus*; mel, *M. melanocephalus*; leuc, *M. leucopterus*. It is common to quantify changes in response to the intensity of selection in terms of units of standard deviation (Lande and Arnold, 1983). Therefore, the changes in morphology can also be compared with the standard deviation for the trait in the species with which the RSD complex shares an ancestor, i.e. *M. grayi* (Figure 1). The standard deviation of morphological traits in *M. grayi* are as follows (mm): female tarsus = 0.6, male tarsus = 0.3; female wing = 1.5, male wing = 2.2; female tail = 2; male tail = 2.2 (Rowley and Russell, 1997). These values give the following mean (\pm SD) standardized inter-node changes: female tarsus = 1.31 (0.61), male tarsus = 2.77 (1.33); female wing = 1.41 (0.88), male wing = 0.97 (0.68); female tail = 1.66 (1.34), male tail = 2.13 (1.27).

the various morphological characters could be assessed by heritability studies.

To confirm the pattern of RSD in fairy wrens and to examine the plausibility of our hypotheses, we analyzed sex, age, morphological, breeding, and behavioral data from an on-going field study of red-backed fairy wrens *M. m. melanocephalus* in Queensland (Karubian J, unpublished data). *M. melanocephalus* live in stable, socially monogamous pairs which are often accompanied by helpers (male offspring which delay dis-

Table 1
Morphology of male and female *Malurus* indicating reversed sexual dimorphism in tail length

Species	Subspecies	Sex	N	Tail (mm)	Tarsus (mm)	Wing (mm)
<i>Malurus leucopterus</i>	<i>leucopterus</i>	M	14	55.8 (2.2)*	19.9 (1.2)	43.7 (1.5)
		F	8	57.6 (1.1)*	19.7 (1.2)	42.4 (1.1)
	<i>leuconotus</i>	M	119	57.4 (2.6)	19.8 (0.8)	47.3 (1.5)*
		F	40	57.6 (1.1)	19.7 (1.2)	45.5 (1.2)*
<i>M. melanocephalus</i>	<i>edouardi</i>	M	10	54.0 (1.9)*	19.5 (0.8)	45.4 (0.9)*
		F	6	56.3 (2.6)*	19.3 (0.6)	44.2 (1.0)*
	<i>melanocephalus</i>	M	52	48.9 (2.6) ^a	20.0 (1.1)	44.0 (1.3)
		F	16	53.3 (3.4) ^b	19.7 (1.4)	43.1 (1.9)
<i>M. alboscapulatus</i>	<i>cruentatus</i>	M	80	40.8 (3.4) ^c	19.1 (0.8)	42.7 (1.5)
		F	32	46.9 (6.3) ^d	19.0 (0.9)	41.6 (1.5)
	<i>alboscapulatus</i>	M	5	41.3 (1.3)*	21.2 (0.5)	50.6 (0.6)*
		F	5	44.3 (2.2)*	21.1 (0.3)	48.8 (0.8)*
	<i>lorentzi</i>	M	7	38.9 (3.7)*	20.4 (1.1)	43.4 (1.0)
		F	6	45.0 (1.8)*	20.0 (0.5)	42.3 (1.3)
	<i>balim</i>	M	6	46.8 (3.9)*	22.3 (0.7)*	50.1 (1.2)*
		F	6	53.0 (2.5)*	21.5 (0.3)*	48.3 (1.2)*
	<i>naimii</i> (lowland form)	M	11	40.3 (2.2)*	20.9 (1.0)	46.8 (1.5)*
		F	10	43.3 (1.9)*	20.3 (0.6)	44.8 (1.4)*
	<i>naimii</i> (highland form)	M	16	46.3 (3.2)*	22.6 (0.6)*	50.1 (1.9)*
		F	18	49.0 (3.0)*	21.6 (0.6)*	48.1 (1.4)*
	<i>aida</i>	M	10	39.4 (2.6)*	21.3 (0.5)	48.9 (2.4)
		F	6	41.8 (2.6)*	21.4 (0.7)	47.5 (0.6)
	<i>randi</i>	M	6	44.2 (2.9)*	22.5 (1.2)	53.2 (2.0)*
		F	4	46.0 (1.8)*	22.5 (1.3)	51.5 (1.3)*
<i>kutubu</i>	M	3	46.3 (0.4)*	23.9 (0.9)	53.0 (0.0)	
	F	4	48.5 (3.5)*	22.8 (0.8)	52.5 (1.3)	
<i>moretoni</i>	M	33	41.8 (3.2)*	21.6 (0.9)	47.9 (2.0)*	
	F	20	44.3 (2.7)*	21.1 (1.1)	46.0 (1.1)*	

Tail = length of the longest tail feather; tarsus = length of the tarsometatarsus; wing = flattened wing length. Values given are means (SD). Sample sizes are as given except for a: $N = 40$; b: $N = 9$; c: $N = 63$; d: $N = 20$. We reconstructed normal distributions of size data based on the population mean, standard deviations, and sample sizes published in Rowley and Russell (1997) and tested for differences between the sexes using two-sample t tests; average t and p values were calculated from 100 repeated simulations of each population.

* Significant difference ($p < .05$) between the sexes.

persal from their natal territory to assist their parents with subsequent reproductive efforts). Helper males retain dull, femalelike plumage until they obtain their own breeding territory, which usually occurs by 2 years of age (Rowley and Russell, 1997; Karubian J, unpublished data).

Our analysis of among-individual morphological data from *M. melanocephalus* revealed significant sexual dimorphism in adult (>1 year old) wing length, tarsus length, and body mass; males are larger and heavier than females (male wing length = 40.93 ± 0.96 mm, $N = 50$, female wing length = 40.47 ± 1.01 mm, $N = 39$, $t_{87} = 2.18$, $p = .032$; male tarsus length = 20.97 ± 0.81 mm, $N = 37$, female tarsus = 20.36 ± 0.91 mm, $N = 23$, $t_{42} = 2.63$, $p = 0.012$; male mass = 7.71 ± 0.67 g, $N = 51$, female mass = 7.05 ± 0.97 g, $N = 35$, $t_{84} = 3.70$, $p < .001$). However, adult male red-backed fairy wrens have significantly shorter tails than females during the breeding season (male breeding tail length = 47.28 ± 4.31 mm, $N = 37$, female breeding tail length = 52.25 ± 6.66 mm, $N = 31$, $t_{66} = 3.71$, $p < .001$) but not during the nonbreeding season (male nonbreeding tail length = 57.90 ± 5.87 mm, $N = 10$, female nonbreeding tail length = 55.92 ± 2.82 mm, $N = 6$, $t_{14} = 0.77$, $p = .46$). In addition, tail lengths of adult males that are socially dominant in a group (and older; Karubian J, unpublished data) are significantly shorter than tail lengths of subordinate males (tail length for breeding males = 47.38 ± 4.32 mm, $N = 44$; tail length for helpers = 52.26 ± 2.94 mm, $N = 4$; $t_{46} = 2.20$, $p = .033$).

Morphology is known to vary with age and social status, as well as sex, in many species of fairy wrens (Schodde, 1982). Therefore, to minimize the influence of age and social status on sexual dimorphism, we also analyzed within-individual changes in tail length and wing length between the nonbreeding and breeding season for adult males ($N = 11$) and females ($N = 9$) (tarsus length does not alter seasonally, but males possessed longer tarsi than females; $t_{18} = 3.13$, $p = .008$). These data corroborate the among-individual sample. Males had longer wings in both the breeding ($t_{18} = 4.39$, $p < .001$) and nonbreeding season ($t_{18} = 2.95$, $p = .009$). Males possessed shorter tails than females in the breeding season, but there was no sexual dimorphism in tail length during the nonbreeding season (Figure 3).

Hence, RSD in tail length is found only in the breeding season. This is consistent with our hypothesis 1 (sexual selection), but inconsistent with hypothesis 3 (similar selection on males and females). For hypothesis 2 (flight energetics) to be valid, flight demands must be higher in males than in females in the breeding season but not at other times of the year. Most empirical data suggest that flight demands are higher for breeding females, as they experience the increased physiological and energetic demands of egg production and flying while gravid (Carey, 1996). However, breeding male red-backed fairy wrens often make long flights (>400 m) between breeding territories, whereas females and secondary males do not. In 500 focal samples conducted during the 1997–1998

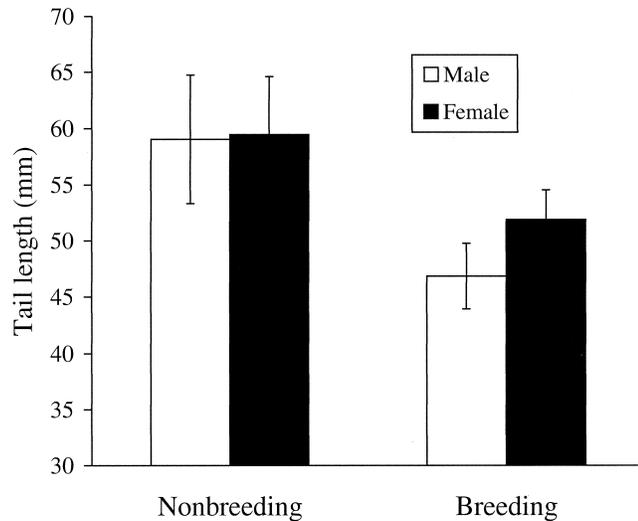


Figure 3

Mean tail length (mm) \pm SD in male (hollow bars, $N = 11$) and female (filled bars, $N = 9$) red-backed fairy wrens, in both breeding and nonbreeding plumage. This species exhibits two molts per year, before and after the breeding season. Tails of both males and females are shorter in the breeding season ($F_{1,18} = 116.82$, $p < .001$), but the reduction in tail length varies between the sexes (sex-by-season interaction from a repeated-measures ANOVA: $F_{1,18} = 6.42$, $p = .021$). Tail length in males is shorter than that in females when the males are in breeding plumage ($t_{18} = 3.36$, $p = .0035$) but not when the males are in nonbreeding plumage ($t_{18} = 0.19$, $p = .85$).

breeding season, males in nonbreeding plumage and females were never observed to leave their territory. Males in bright plumage, however, left the territory an average of 0.4 times per 30-min observation period to intrude upon other breeding territories (Karubian J, unpublished data). Males presumably make such forays in search of extrapair mates. As fairy wrens are notoriously poor fliers and rarely fly for extended periods of time (most of their locomotion involves hopping or taking short flights between foraging sites; Schodde, 1982), these observations indicate that biomechanical considerations could explain the reduction in male tail length during the breeding season. It will be important to directly quantify the flight costs of different tail morphologies in these and closely related species.

Whichever mechanism accounts for the RSD in tail length of this group of fairy wrens, this novel evolutionary pattern has implications for evolutionary theory. The reported pattern suggests that reduced trait size can be the selected ornamental trait in birds. We are aware that this pattern of male tail shortening also occurs in *Cisticolas* (Lewis M, unpublished data), although there are as yet no published reports. All other reported incidences of sexual dimorphism in tail length have presumed tail elongation in one sex (most commonly the male; Andersson, 1994). This is clearly not the case in fairy wrens, and hence other reports of tail elongation should be evaluated within a phylogenetic framework to indicate the magnitude and direction of changes in tail length. Without a phylogenetic approach we could have equally assumed that female tail length was increasing and hypothesized that females were the ornamented sex. In addition, current accepted wisdom proposes that increased ornament size increases trait costs and enforces honesty upon trait design (Zahavi, 1975). If tail length differences are used as a signal in fairy wrens,

this system would provide a fascinating test (and potential contradiction) of the handicap theory.

Although the functional importance of the fairy wren tail is not yet clear, our data support the notion that the shortened male tail is advantageous during the breeding season and that there is selection for decreased male tail length in these species. The pattern of RSD in this fairy wren complex is also novel in that it provides evidence that sexually dimorphic selection pressures can act in the opposite direction in body size (tarsus and wing length) and tail length within a species. Most evolutionary explanations of sexual dimorphism have assumed that directional selection acting on the size of one trait will tend to drag along other traits through genetic correlations (Lande, 1980; Lande and Arnold, 1983). Tarsus and wing length are good indicators of body size in birds; hence selection appears to be acting in opposite directions (relative to females) for male body size and male tail length. Therefore, our findings indicate that current models for the evolution of sexual dimorphism are not comprehensive and that tail length RSD in the fairy wrens can provide a novel system in which to test sexual selection theory.

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