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Racketed tail of the male and female turquoise-browed motmot: male but not female tail length correlates with pairing success, performance, and reproductive success

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Abstract Both males and females of many avian species maintain elaborate plumage traits, and elaborate monomorphic plumage may convey adaptive benefits to one or both sexes as inter- or intraspecific signals. Both sexes of the turquoise-browed motmot (*Eumomota superciliosa*) are elaborately plumed with long racket-tipped tail. I investigated whether the racketed tail functions as a sexually selected signal in one or both sexes by testing the predictions that males and/or females with the largest tails have: (1) greater pairing success, (2) greater reproductive performance (clutch-initiation date, clutch size, and hatching success), and (3) greater reproductive success. Yearling males with longer denuded rachises (wires) on the central tail feathers had greater pairing success. In addition, adult males with longer wires paired with females who laid larger clutches, had greater hatching success independent of clutch size, and fledged more young. There was no relationship between female tail plumage and pairing success, reproductive performance, or fledgling success. These results are consistent with the hypothesis that male tail plumage functions as a mate choice or status signal, but that the tail of the female does not function in a sexually selected context. I discuss

alternative hypotheses for the evolutionary maintenance of the elaborate female tail plumage.

Sexual selection generally operates more strongly on males than on females, resulting in greater elaboration of secondary sexual traits among males. However, there are many species where both sexes are elaborate often to a very similar degree (elaborate monomorphic). A diverse array of avian taxonomic groups express elaborate traits in both sexes (e.g., coloration: parrots, waxwings, and orioles; head feathers: penguins, grebes, and alcids; tail feathers: swallows, parrots, and motmots), and these groups are of great interest because elaborate female traits are difficult to reconcile within the traditional framework of sexual selection, which assumes that one sex is much more competitive than the other sex (for review, see Amundsen and Pärn 2006).

Elaborate monomorphic traits can function in both sexes during competition for access to mates as mate-choice signals, as status signals, or both (mutual sexual selection hypothesis, Jones and Hunter 1993, 1999). This hypothesis proposes that the most ornamented males and females are more successful at acquiring high-quality mates (Johnstone et al. 1996; Johnstone 1997; Amundsen 2000a,b). Similarly, elaborate monomorphic traits can function as status signals in competition for nonsexual resources (social selection hypothesis, West-Eberhard 1979, 1983). Unlike status signals that function during competition for mates, socially selected status signals function in contests for access to nonmate resources such as food, foraging sites, or

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territories (Rohwer 1975; Heinsohn et al. 2005; Senar 2006). In this paper, I combine these two hypotheses and will refer to elaborate traits that confer sexually or socially selected benefits as sexually selected traits. This convention is adopted because most predictions of the two hypotheses are similar, and because I do not attempt to separate these selective forces. Consistent with these hypotheses for the maintenance of elaborate monomorphism, research has shown that elaborate traits are related to male and female mate preference (Jones and Hunter 1993; Arnold et al. 2002; Hill 1993, 2002; Torres and Velando 2005), pairing success (Daunt et al. 2003), reproductive success (Ruusila et al. 2001; Massaro et al. 2003), various measures of individual quality (phenotypic condition, Velando et al. 2001; survival, Hõrak et al. 2001; dominance, Kraaijeveld et al. 2004), and to assortative pairing (Andersson et al. 1998; Jawor et al. 2003; Safran and McGraw 2004).

In contrast, elaborate monomorphic traits can be functional only in males as mate-choice or status signals, and females can express nonadaptive 'male-like' traits as by-products of genetic correlation between the sexes (genetic correlation hypothesis; Darwin 1871; Lande 1980, 1987). This hypothesis serves as the null hypothesis in investigations into the function of elaborate female traits (for review, see Amundsen 2000a) and has received support from studies that have found no evidence of sexual selection maintaining elaborate female traits (Hill 1993; Cuervo et al. 1996; Muma and Weatherhead 1989; Wolf et al. 2004).

Alternatively, elaborate monomorphic traits can be maintained by natural selection and function for utilitarian purposes (natural-selection hypothesis). Natural selection can favor elaborate traits that serve a myriad of purposes among birds, including aerodynamic structures that aid in flight (Balmford et al. 1993) and a diverse range of intraspecific signals, such as signals of aposematism (Dumbacher et al. 1992), signals to startle prey to facilitate foraging (Mumme 2002), signals to distract predators from nests (Deane 1944), signals to disorient predators during attack (Palleroni et al. 2005), and signals to deter predator pursuit (Woodland et al. 1980) or predator ambush (Murphy 2006, 2007a).

Both sexes of the turquoise-browed motmot (*Eumomota superciliosa*) have long tails that comprise approximately 60% of the total body length and terminate in large blue and black rackets. This species has the longest region of bare rachis (wire) on the two racketed-tail feathers, which are denuded of feather barbs for almost half the feather's length. The unique rackets develop when weakly attached barbs along the wire fall off because of abrasion with natural substrates and routine preening (Beebe 1910; Wagner 1950; Murphy 2005). The distinct racketed tail typifies the Momotidae, and the turquoise-browed mot-

mot's tail is the most elaborate among the ten species within the family (Forshaw and Cooper 1987; Snow 2001; Skutch 1947).

In previous research (Murphy 2006, 2007a), I demonstrated that both males and females perform a side-to-side wag display with their long racketed tails in the presence of predators. Results from predator presentation experiments showed that the predator was the likely receiver of the signal, and data were consistent with the hypothesis that the wag display deters predators from attempting to ambush the signaler. Although these results support the natural selection hypothesis for the evolutionary maintenance of the male and female tail, this does not rule out the possibility that the tail also functions as a sexually selected signal. Indeed, the extraordinary appearance of the tail suggests its use as a sexual signal, and Darwin (1871, edition 2, p. 404) spoke of the possible ornamental value of the 'spoon-like' tail of the turquoise-browed motmot in his discussion of sexually selected traits. In another study (Murphy 2007b), I addressed the potential role of the turquoise-browed motmot's tail as a sexually selected signal in both sexes by testing for assortative mating. I found no evidence for assortative mating for tail size in correlative studies or in an experimental mate-removal study. The lack of assortative pairing in this species suggests that the tail is not sexually selected in both males and females; however, this research did not address the possibility that only one sex may gain a sexually selected benefit from the maintenance of the elaborate racketed tail.

In the current study, I examine the potential role of sexual selection in maintaining the elaborate male and female tail. I test if the size of the tail correlates with male and female: (1) pairing success, (2) reproductive performance, and (3) fledgling success.

Materials and methods

Study site and study organism

I studied the turquoise-browed motmot (*E. superciliosa*) near the Ria Lagartos Biosphere Reserve in northern Yucatan, Mexico (21°33′N, 88°05′W) from March to August 1999–2002. The turquoise-browed motmot breeds colonially and nests in tunnels dug in earthen banks (Orejuela 1977). I studied motmots at four colonies located in abandoned limestone quarries (range=7–39 pairs) located within a 10-km^2 area.

The turquoise-browed motmot is socially monogamous. Both males and females incubate and brood (Scott and Martin 1983), and both sexes provision highly dependent altricial chicks (clutch size, $X\pm SD=4.0\pm0.6$; range 3–6; $N=232$). Most pairs successfully produce at

least one fledgling ($X \pm \mathrm{SD} = 2.5 \pm 0.9$, range 1–5, $N=169$), and the species fledges a maximum of one brood per year.

In the northern Yucatan, the turquoise-browed motmot is migratory. Both males and females return to the breeding areas at the same time in early March, approximately 3 months before clutch initiation. Survival among adult territorial birds is high (88%) and divorce uncommon (21%; unpublished data). Most individuals who bred the previous year arrive already paired, although pair bonds shuffle as new individuals arrive and compete for nesting territories or partners. Each year, some individuals of both sexes fail to pair. Unpaired birds are generally not transient and, like breeding birds, remain at one colony throughout the breeding season.

General methods

Each year, motmots were captured with mist nets placed around the colony during a 1.5-month period. Capture efforts began after birds had established pair bonds and nest ownership and ended before clutch initiation. At each of the four colonies, 95% of all breeders and approximately 85% of floaters were captured and banded with individually recognizable color bands. All birds were sexed by laparotomy, and there were no noticeable adverse affects of the procedure; laparotomized individuals were observed behaving normally the following day. Behavioral observations were conducted with spotting scopes from within permanent blinds located 45–55 m from nesting colonies.

Morphological measurements

Morphological measures were taken from all birds in 1999–2002. Mass was measured with a Pesola scale to the nearest 0.5 g. Linear measures were taken to the nearest 0.1 mm with calipers or with a ruler. I measured tarsus length, bill length, and flattened wing length, and these values were combined using principal components analysis to compute a single body size index. The first principal component (PC1) explained 53% of the variation in body size. Tarsus length, bill length, and flattened wing length loaded positively on the PC1 axis (eigenvectors=0.56, 0.59, and 0.59, respectively). I also measured six linear components of the tail (Fig. 1): (1) total tail (central follicle to the distal tip of the longest central rectrix), (2) racket (sum of the wire [rachis devoid of barbs] and the flag [oval-shaped tip]), (3) base (central follicle to the distal tip of the longest second tail feather), (4) wire (rachis devoid of barbs between the base and the flag on the longest central rectrix), (5) blue of flag (blue portion of the flag on the longest central rectrix), and (6) black of flag (the black portion of the flag on the longest central rectrix).

I also measured the surface area of the oval-shaped tip of the largest flag, herein referred to as (7) flag area. In 2002, I photographed feathers using standardized digital photography. Surface area was later calculated with the ImageJ Software Package (US National Institutes of Health 1997–2006). Flag area was calculated for other years by multiplying the length of the flag by its linear width and a constant. The calculated measures were significantly and highly correlated with the measures taken from photographs ($F_{1,\ 320}=1{,}575.25$, $P<0.0001$, $R^2=83.0$). Thus, the two types of measures were considered equivalent, and calculated measures were used when photographic measures were unavailable.

I collected all morphological measures. Repeatability (the intraclass correlation coefficient; Lessells and Boag 1987) of all morphological measurements was calculated on a subset of birds in 2002 by measuring the same individual on different days. Repeatability was high for all linear measures of body size and tail components ($N=12$, all $F>360.0$, all $P<0.0001$, all $r\geq0.99$) and for surface area ($F_{1,\ 10}=48.02$, $P=0.0001$, $r=0.89$).

Pairing success

I monitored pairing success of all banded individuals and classified them as either paired or unpaired depending on whether they successfully initiated a clutch. To minimize the chance that birds classified as unpaired actually bred elsewhere, I only considered individuals as unpaired if they were observed regularly after the ultimate primary clutch of the season was initiated.

I analyzed pairing success of adults and yearlings separately because there was little variation in adult breeding success (the majority of adults bred each year), whereas only some yearlings bred each year (unpublished data).

Reproductive performance

I quantified clutch-initiation date, clutch size, and hatching success by checking nest contents every 2–4 days with a lipstick-shaped camera attached to the end of a flexible hose. The camera was illuminated by an infrared light source, and the image was displayed on a small television. Clutch-initiation date was defined as the date the first egg appeared in the nest. In some cases, the clutch-initiation date was backwards calculated based on the species-specific 48-h laying pattern (Scott and Martin 1983). Because the multiple years' data were combined, clutch-initiation date was z-score-standardized for each year. Clutch size and hatching success were defined as the maximum number of eggs and nestlings observed within each nest.

Fig. 1 Tail components of the turquoise-browed motmot. The *horizontal lines* show the linear distance measured for each tail component. Flag area is the surface area of the *oval-shaped* tip

Total Tail
Racket
Base
Wire
Blue of Flag
Black of Flag
Flag Area
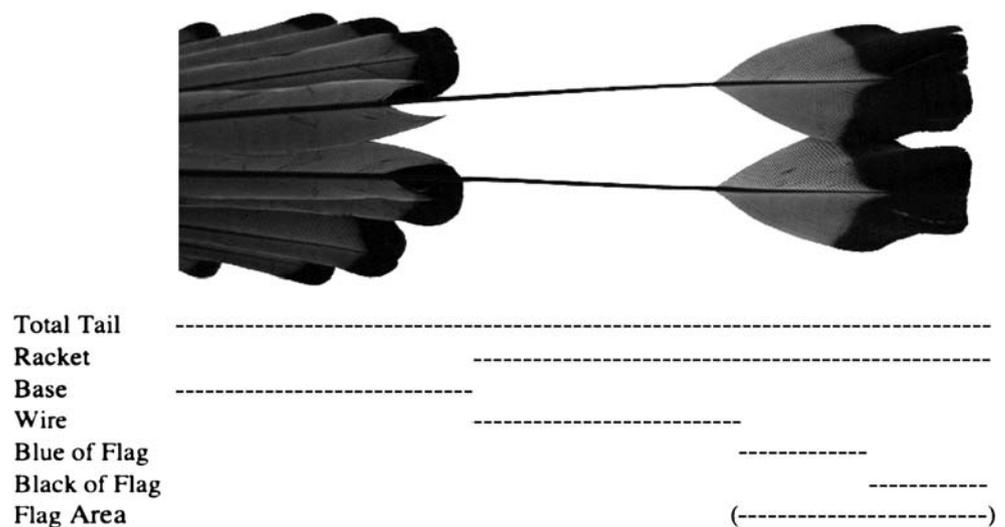
Fledging success

Adult fledging success was analyzed in two ways: (1) whether a pair did or did not fledge, and (2) how many fledglings were produced from successful nests. I considered birds to have fledged if nestlings survived to at least 24 days of age, which is the earliest reported age for fledging in this species (Orejuela 1977; Scott 1984).

Statistics

Because body size is correlated with the size of many tail components (Murphy 2007b), I standardized each tail component for body size by calculating residual values from regressions of each tail component on body size (PC1; calculated separately for sexes). Both residual values of tail components and actual morphological measures were used in all analyses testing the function of tail plumage. To control for the potential effects of tail-feather loss on dependent variables, I excluded birds that lost or damaged both central tail feathers before they initiated their first clutch of the season.

All analyses were conducted using combined data set from 2000 to 2002, except for pairing success, which was analyzed using a data set from 2000 and 2002 (a manipulative experiment not reported here was conducted in 2001). When combining data from multiple years, I analyzed the most recent year's data for each individual to avoid pseudoreplication.

Statistical analyses were conducted using JMP software (SAS Institute, Cary, NC, 1989–2006). Multiple logistic regression was used to investigate the relationship between tail plumage and pairing success and between tail plumage and whether individuals fledged at least one young. Multiple linear regression was used to investigate the

relationship between tail plumage and clutch-initiation date, clutch size, hatching success, and number of fledglings. Independent variables in all models included year, colony, and all tail components (total tail, base, wire, blue of flag, black of flag, and flag area). Independent variables were removed one-at-a-time from the model, largest P values first, until all effects had $P<0.10$. All models were run separately for the sexes. Normality of data sets was confirmed by visual inspection. All statistical analyses were two tailed, and rejection level was $\alpha>0.05$.

Results

Pairing success

The proportion of unpaired birds was higher among yearlings than adults. Among males, 74% of yearlings were unpaired ($N=23$), whereas 5% of adults were unpaired ($N=98$). Among females, 60% of yearlings were unpaired ($N=30$), whereas 3% of adults were unpaired ($N=98$). Thus, most unpaired birds were yearlings (unpaired males, 77% yearling [$N=22$]; chi-square test, $\phi_1^2=6.91$, $P=0.009$; unpaired females, 86% yearling [$N=21$]; chi-square test, $\phi_1^2=11.89$, $P<0.001$). There was a 1:1 sex ratio of unpaired birds (22:21).

Pairing success of yearling males was significantly positively correlated with residual wire (Tables 1 and 2), and results were not qualitatively different when the analysis was performed using measures not standardized for body size ($\phi_1^2=4.49$, $P=0.034$). In contrast, pairing success among yearling females was not significantly correlated with tail components (Tables 1 and 2). Among adult males and females, pairing success was not significantly correlated with tail components (Tables 1 and 2).

Table 1 Significant predictors of male and female pairing success, reproductive performance, and reproductive success from logistic regression models

	Male				Female	
	Significant predictors	χ^2	P	N	Significant predictors	N
Yearling pairing success	Wire	5.23	0.022	25	None	31
Adult pairing success	None	–	–	80	None	65
Y/N fledged	None	–	–	75	None	62

The model was constructed using seven tail components (standardized to body size), colony, and year as independent variables. Dependent variables are listed along the left. The probability to leave the model was $P>0.10$.

Reproductive performance

Many measures of reproductive performance and fledging success were intercorrelated (Table 3). Clutch size was significantly positively correlated with hatching success and fledging success; and hatching success was strongly and significantly correlated with fledging success (Table 3).

Clutch-initiation date was not significantly correlated with male tail components or with female tail components (Tables 1 and 2). However, clutch size was significantly positively correlated with male residual wire (Tables 1 and 2), and results were not qualitatively different when the analysis was performed using measures not standardized for body size ($F_{1, 64}=6.33$, $P=0.014$, $R^2=0.09$). In contrast, clutch size was not significantly correlated with female tail components. In addition, hatching success was significantly positively correlated with male residual wire (Tables 1 and 2), and results were not qualitatively different when the analysis was performed using measures not standardized for body size ($F_{1, 49}=10.52$, $P=0.002$, $R^2=0.18$). In contrast, hatching success was not significantly correlated with female tail components.

When clutch size was added to the model to control for the effect of egg number on hatching number, the effect of male wire on hatching success remained significant ($F_{1, 48}=16.95$, $P<0.0001$, $R^2=0.39$; clutch size, $P<0.0001$; wire, $P=0.041$), and female tail components remained not significantly correlated with hatching success.

Fledging success

Success at producing at least one fledgling was not significantly correlated with male tail components or with female tail components (Tables 1 and 2). However, the number of fledglings produced from successful nests was significantly positively correlated with male residual wire (Tables 1 and 2), and results were not qualitatively different when the analysis was performed using measures not standardized for body size ($F_{6, 53}=4.99$, $P<0.001$, $R^2=0.29$; wire, $P=0.007$l; year, $P=0.004$; colony, $P=0.003$). In contrast, the number of fledglings was not significantly correlated with female tail components, although females with longer wires tended to produced fewer fledglings ($F_{1, 45}=3.66$, $P=0.062$; $R^2=0.08$).

Discussion

There is no evidence that the mutual sexual selection maintains the elaborate racketed tail of both the male and female turquoise-browed motmot. However, two lines of evidence are consistent with the hypothesis that the male's

Table 2 Significant predictors of male and female pairing success, reproductive performance, and reproductive success from multiple regression models

	Male					Female	
	Significant predictors	F (df)	P	N	R^2_{adj}	Significant predictors	N
Clutch-initiation date	None	–	–	72	–	None	58
Clutch size	Wire	8.54 (1, 64)	0.005	66	0.12	None	53
Hatching success	Wire	9.66 (1, 49)	0.003	51	0.16	None	39
Number of fledglings	Model	5.05 (6, 53)	<0.001	60	0.29	None	47
	Wire	–	0.006	–	–		
	Year	–	0.002	–	–		
	Colony	–	0.003	–	–		

The model was constructed using seven tail components (standardized to body size), colony, and year as independent variables. Dependent variables are listed along the left. The probability to leave the model was $P>0.10$.

Table 3 Product moment correlations between and among measures of reproductive performance and fledgling success

Variable	By variable (number)	Correlation	N	P	Significance
Clutch-initiation date	Number of eggs	−0.12	76	0.28	NS
Clutch-initiation date	Number of hatch	−0.08	58	0.56	NS
Clutch-initiation date	Number of fledglings	−0.08	65	0.54	NS
Number of eggs	Number of hatch	0.53	58	<0.0001	[a]
Number of eggs	Number of fledglings	0.35	61	0.0059	[a]
Number of hatch	Number of fledglings	0.57	56	<0.0001	[a]

[a] Significance indicated after sequential Bonferroni correction

racketed tail is maintained by sexual selection. First, pairing success was positively related to male but not to female tail size. Yearling males with long wires (denuded rachises on the central tail feathers) were more successful at acquiring a mate and initiating a clutch than the yearling males with short wires. Although no relationship between tail and pairing success was detected among adults, there was limited statistical power because of the small variance in adult pairing success (i.e., most adults successfully paired). It is worth noting that the mean wire of yearling males who paired was similar to the mean wire of adult males. This similarity may indicate that there is a minimal wire length, below which a male is very unlikely to gain access to a mate. Among females, tail components were not correlated with pairing success, and the lack of relationship between female tail components and pairing patterns agrees with an earlier study on this species that demonstrated a lack of assortative pairing for tail components (Murphy 2007b).

Second, reproductive success was positively related to male but not to female tail size. Males with longer wires fledged significantly more young, whereas there was a trend for females with longer wires to fledge fewer young. Previous research on this species has demonstrated that male and female tail components increase in size between the first year of life (yearling) and second year of life but do not increase with age thereafter (Murphy 2007b). Thus, the positive correlation between wire length and reproductive success in adult males is not due to age-related differences in tail expression.

Male wire length positively related to his partner's clutch size and to hatching success. Thus, it appears that males with longer wires experienced greater reproductive success because they paired with females who laid larger clutches. This interpretation is consistent with the findings that much of the variance in fledgling success is explained by clutch size and hatching success. It is possible that females paired to more ornamented males are in better physical condition and are thus able to expend more resources into laying more or higher quality eggs. If true, it remains unclear how the process of pair formation brings together males with long wires and females who invest more into their clutches. One possible explanation is that higher quality females prefer

more ornamented males, and these females are also more likely to gain access to these more ornamented males. Alternatively, males with longer wires may gain reproductive benefits if females invest more into reproduction when they are paired to an attractive male (differential allocation hypothesis, Burley 1986). If either of these mechanisms represent the means by which males with long wires achieved higher reproductive success, these results are consistent with the Darwin–Fisher mechanism of sexual selection in monogamous species (Darwin 1871; Fisher 1958; Kirkpatrick et al. 1990), whereby more ornamented males gain a selective advantage by pairing with females with greater reproductive success (O'Donald 1980; Møller 1994).

I did not assess reproductive success using genetic techniques because it was extremely difficult to remove chicks from their long tunnel nests. If extra pair copulations (EPCs) are common in this species, sexual selection on tail length could either be weaker or stronger than suggested by my measures of social mating success. Males with long wires may suffer a disadvantage in the EPC arena, despite their social mating advantage, but this result seems unlikely. It seems more likely that females would seek males with long wires as social mates and for EPCs, and that sexual selection for male tail length may in fact be stronger than suggested by social mating success. Future research on this species should try to measure extra-pair paternity to clarify whether males with longer wires experience greater genetic mating success.

A handful of studies on the adaptive significance of elaborate monomorphic traits have supported the sexual selection hypothesis for only males and have found no benefits associated with elaborate female traits (Hill 1993; Cuervo et al. 1996; Muma and Weatherhead 1989; Wolf et al. 2004). These studies have concluded that the genetic correlation hypothesis, which was the null, was likely to account for the expression of what the authors interpreted as nonfunctional female traits (but see Hill 2002 for updated results). Likewise, I found no evidence for sexual selection on female tails; however, previous work (Murphy 2006, 2007a) showed that both sexes are likely to gain adaptive benefits in a nonsexually selected context by displaying their tail in a

pendulum-like fashion (wag display) upon encountering a predator. This research experimentally showed a link between the presence of a predator and the performance of the wag display and suggested that the wag display is not directed at conspecifics but is instead directed to the predator and communicates awareness to deter pursuit or ambush. The use of the elaborate tail by both sexes as a pursuit-deterrent signal strongly argues against the hypothesis that the tail is expressed solely as a nonfunctional by-product of genetic correlation. I thus propose that selection on the male and female tail is twofold, that natural selection maintains the long racketed tail in males and females for effective pursuit-deterrent signaling, and that sexual selection on males selects for a more elaborate male tail. The moderate sexual dimorphism in the wire (approximately 10%; Murphy 2007b) supports this hypothesis.

Further research is needed to establish whether the combined effects of natural and sexual selection represent a widespread yet underappreciated pathway to the maintenance of elaborate monomorphic traits. In support of this hypothesis, elaborate monomorphic tail streamers of the barn swallow have been shown to assist with flight (Buchanan and Evans 2000) and to also function in males as a sexual signal (Møller et al. 1998). Interestingly, the shorter tail streamers of female barn swallows are thought to represent the naturally selected optimum to aid in aerodynamic lift (Hedenström and Møller 1999). As another example, many male African antelope have long horns that function during intersexual competition for access to mates, and females gain no sexually selected benefits from the expression of smaller 'male-like' horns (Geist 1966). However, female antelope use their smaller horns to drive away predators from their offspring (Packer 1983). I suggest that the typical two-hypothesis framework adopted by studies into the adaptive significance of elaborate monomorphic traits (mutual sexual selection and genetic correlation) is too restrictive and should be revised to include the hypothesis that natural selection, or a combination of natural and sexual selection, can also contribute to the maintenance of elaborate traits in both sexes.

Correlational data presented here are consistent with the hypothesis that the tail of the male turquoise-browed motmot is a sexually selected signal, and that the similarly elaborate female tail is not maintained by sexual selection. To better understand the extent to which sexual selection plays a role of the maintenance of the male tail, future research should include experimental manipulation of the male tail in order to elucidate its role in inter- or intrasexual competition.

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