

2008

Lack of Assortative Mating for Tail, Body Size, or Condition in the Elaborate Monomorphic Turquoise-Browed Motmot (*Eumomota superciliosa*)

Troy G. Murphy
Trinity University, tmurphy@trinity.edu

Follow this and additional works at: https://digitalcommons.trinity.edu/bio_faculty

Part of the [Biology Commons](#)

Repository Citation

Murphy, T. G. (2008). Lack of assortative mating for tail, body size, or condition in the elaborate monomorphic turquoise-browed motmot (*Eumomota superciliosa*). *Auk*, 125(1), 11–19. doi:10.1525/auk.2008.125.1.11

This Article is brought to you for free and open access by the Biology Department at Digital Commons @ Trinity. It has been accepted for inclusion in Biology Faculty Research by an authorized administrator of Digital Commons @ Trinity. For more information, please contact jcostanz@trinity.edu.



LACK OF ASSORTATIVE MATING FOR TAIL, BODY SIZE, OR CONDITION IN THE ELABORATE MONOMORPHIC TURQUOISE-BROWED MOTMOT (*EUMOMOTA SUPERCILIOSA*)

TROY G. MURPHY¹

Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA

ABSTRACT.—Elaborate male and female plumage can be maintained by mutual sexual selection and function as a mate-choice or status signal in both sexes. Both male and female Turquoise-browed Motmot (*Eumomota superciliosa*) have long tails that terminate in widened blue-and-black rackets that appear to hang, unattached, below the body of the bird. I tested whether mutual sexual selection maintains the Turquoise-browed Motmot's elaborate tail plumage by testing the prediction that mating occurs in an assortative manner for tail plumage. I also tested whether assortative mating occurs for body size, a potential measure of dominance, and for phenotypic condition, a measure of individual quality. Assortative mating was measured (1) within all pairs in the study population, (2) within newly formed pairs, and (3) within experimentally induced pairs that formed after removal of females from stable pairs. Assortative mating was not found for tail plumage, body size, or phenotypic condition in any of these samples. Therefore, there was no support for the “mutual sexual selection” hypothesis. I discuss the hypothesis that the tail is sexually selected in males only, and that natural selection accounts for the evolutionary maintenance of the elaborate female tail. *Received 13 September 2005, accepted 29 August 2006.*

Key words: assortative mating, elaborate monomorphism, *Eumomota superciliosa*, mutual ornamentation, sexual selection, tail plumage, Turquoise-browed Motmot.

Ausencia de Apareamiento Asociativo con Respecto a la Cola, el Tamaño Corporal o la Condición en *Eumomota superciliosa*

RESUMEN.—La existencia de plumaje elaborado en los machos y las hembras puede ser mantenida por selección sexual mutua, y funcionar como una señal para la selección de parejas o del estatus de los individuos en ambos sexos. Tanto los machos como las hembras de la especie *Eumomota superciliosa* tienen colas largas que terminan en unas raquetas ensanchadas de color azul y negro, que parecen colgar debajo del cuerpo de las aves. En este estudio probé si el plumaje elaborado de la cola de esta especie es mantenido mediante selección sexual mutua, evaluando la predicción de que el apareamiento es asociativo con respecto al plumaje de la cola. También probé si existe apareamiento asociativo con respecto al tamaño (una medida potencial de la dominancia) y con respecto a la condición fenotípica (una medida de la calidad de los individuos). El apareamiento asociativo fue medido para todas las parejas de la población de estudio, para parejas formadas recientemente y para parejas cuya formación fue inducida experimentalmente mediante la remoción de las hembras de parejas estables. No se encontró apareamiento asociativo con respecto al plumaje de la cola, al tamaño corporal, ni a la condición fenotípica en ninguna de estas muestras. Por lo tanto, no existió respaldo para la hipótesis de selección sexual mutua. Discuto la hipótesis que plantea que la cola es objeto de selección sexual sólo en los machos, y que la selección natural permite explicar el mantenimiento evolutivo de la cola elaborada en las hembras.

MOST RESEARCH INTO the function of elaborate traits has focused on male plumage (Anderson 1994). However, there are many avian species in which both males and females are elaborately plumed (“elaborate monomorphic”), and it remains unclear whether females also generally gain sexually selected benefits from elaborate plumage.

Sexual selection may favor the expression of elaborate traits in males and females when competition for access to mates occurs in both sexes (i.e., mutual sexual selection; Jones and Hunter 1993; Johnstone et al. 1996; Amundsen 2000a, b; Amundsen and Pärn 2006). Competition for mates by both males and females is expected to occur when the potential reproductive rate is similar

¹Present address: Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada. E-mail: tgm3@cornell.edu

for both sexes (*sensu* Trivers 1972, Clutton-Brock and Vincent 1991) and when the operational sex ratio is near unity (*sensu* Emlen and Oring 1977). Under these conditions, neither sex will represent a scarcer resource to be competed for by a limited sex. Because the potential reproductive rate and the operational sex ratio are highly dependent on the relative degree of male and female parental investment, mutual sexual selection operates most strongly in socially monogamous species with biparental care (Burley 1986).

Many investigations into the potential adaptive benefits of elaborate monomorphism have supported the “mutual sexual selection” hypothesis by demonstrating that individuals mate assortatively for elaborate traits (e.g., plumage coloration [Andersson et al. 1998, Safran and McGraw 2004], eye coloration [Massaro et al. 2003], size of colored plumage-patch [Masello and Quillfeldt 2003], tail length [Møller 1993, Regosin and Pruett-Jones 2001, Boland et al. 2004], and other ornamental appendages [Daunt et al. 2003, Kraaijeveld et al. 2004]). Assortative mating for sexually selected traits can occur when individuals choose to mate with the most ornamented mate available, and ornamented individuals accept only ornamented suitors. This leaves less-ornamented individuals to mate among themselves, not because they prefer to mate assortatively, but because their own lack of ornamentation precludes them from mating with more desirable individuals (Burley 1983, Johnstone 1997). Assortative mating can also result if elaborate traits function in both sexes as status signals, as males and females compete with same-sex rivals to gain access to the same resources (Creighton 2001).

I investigated the adaptive significance of the elaborate tail of the male and female Turquoise-browed Motmot (*Eumomota superciliosa*; hereafter “motmot”), a colonial-breeding, socially monogamous species that exhibits biparental care. The long tail comprises ~60% of the total body length and terminates in widened, blue-and-black rackets, which appear to hang unattached below the body of the bird (Fig. 1). The apparent detachment occurs because the rachises of the central rectrices (wires) are devoid of barbs for approximately one-third of the feather above the terminal racket-flags. The wires develop because feather barbs fall off from abrasion with natural substrates or during routine preening (Beebe 1910, Wagner 1950, Murphy 2007b).

Both sexes display their racketed tails in a wag-display, repeatedly rocking the tail from side to side in a regular motion similar to that of a pendulum. Previous research has demonstrated that the wag-display is not performed in mating contexts, but is instead performed in the presence of predators, and behavioral data support the hypothesis that the wag-display functions as a pursuit-deterrent signal (Murphy 2006, 2007a). In addition to this naturally selected pursuit-deterrent function of the tail, research has demonstrated that sexually selected benefits are associated with male tail length, but not female tail length: males with longer wires have greater pairing success, pair with females that lay larger clutches, and have greater fledgling success (Murphy 2007c). By contrast, female tail length is not related to measures of performance and reproductive success, which suggests that sexual selection does not account for the maintenance of the elaborate female tail.

To further investigate whether the racketed tail functions as a sexually selected signal in males and females, I tested whether mating occurs assortatively for tail plumage. I first measured the

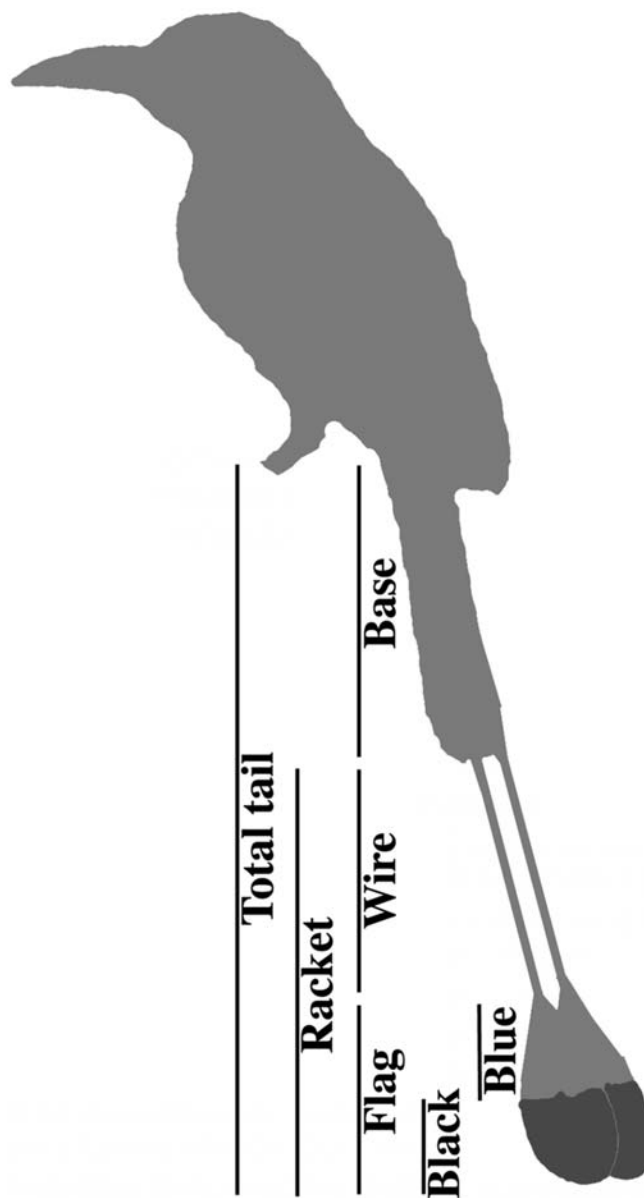


FIG. 1. Seven tail components of the Turquoise-browed Motmot.

similarity of tail plumage within paired birds for all pairs in the study population. Second, I measured similarity of tail plumage within newly formed pairs. Because the pool of available mates is limited each season because of high mate fidelity (Murphy 2007c), this second analysis increased detectability of assortative mating by focusing only on the distribution of tail plumage within the limited pool of available mates. In addition to these correlative studies, I experimentally removed females from stable pairs and monitored whether males paired assortatively for tail plumage with replacement females. In all the above samples, I also investigated mating patterns for body size, a potential measure of dominance, and for phenotypic condition, a measure of individual quality.

METHODS

Study organism and study site.—Motmots breed colonially in the Yucatan Peninsula of Mexico, in sinkholes and man-made structures such as freshwater wells (Orejuela 1977, Scott and Martin 1983). Colonies range in size from 2 to 60 pairs, with colonies of 10–20 pairs being most common (Orejuela 1977, Murphy 2005). Nest tunnels are dug into vertical earthen banks (0.4–2.2 m in depth; mean = 1.3 m).

I studied motmots at seven colonies during the breeding seasons (March–August) of 1999–2002, four in abandoned limestone quarries (range: 7–39 pairs), and three in freshwater wells (range: 20–30 pairs). All colonies were located within a 10-km² area near the Ria Lagartos Biosphere Reserve in Northern Yucatan, Mexico (21°33'N, 88°05'W). The area is characterized by thornscrub forest and grazing pastureland and experiences a dry season from December to May.

Motmots are migratory in the Yucatan, and individuals spend six months on wintering grounds, presumably in moist forests in the center of the Yucatan Peninsula. They arrive at the breeding areas in March, three months before clutch initiation. Motmots exhibit high mate fidelity (Murphy 2005), and pairs are often established upon arrival. Unpaired birds generally pair within the first month after arrival.

I captured motmots in mist nets before the start of clutch initiation and determined sex by laparotomy. There were no noticeable negative effects from the procedure: laparotomized individuals were observed at the breeding colonies the following day behaving normally. To facilitate individual identification, most breeders (98%) and nonbreeding floaters (~85%) were color-banded.

Morphology.—Morphological measurements were taken from all birds in 1999–2002. Mass was measured with a Pesola scale to the nearest 0.5 g. Linear measurements 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 component analysis (PCA) 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 (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, referred to here as (7) flag area. In 2002, I photographed feathers using standardized digital photography. Surface area was later calculated with the IMAGEJ software package (U.S. National Institutes of Health 1997–2008). Flag area was calculated in other years by multiplying the length of flag by its linear width and a constant. The calculated measurements were significantly and highly correlated with the measurements taken from photographs ($F = 1,575.25$, $df = 1$ and 320 , $P < 0.0001$, $r^2 = 83.0$). Thus, the two

types of measurements were considered equivalent, and calculated measurements were used when photographic measurements were unavailable.

I collected all morphological measurements. Repeatability (the intraclass correlation coefficient) 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 (all $F > 360.0$, all $P < 0.0001$, all $r \geq 0.99$, $n = 12$) and for surface area ($F = 48.02$, $df = 1$ and 10 , $P = 0.0001$, $r = 0.89$) (Lessells and Boag 1987).

I computed sexual dimorphism of the seven tail components and correlations among the seven measures of tail components with measurements taken in 2002. To investigate whether tail components or body size increased with age, I measured the change in morphology of known-age birds between 2000–2001 and 2001–2002. Between-year changes were measured between the first year of life (yearlings) and the second year of life, and between the second and third year of life.

Phenotypic condition.—I collected five measures of phenotypic condition from each bird. (1) Size-specific mass, an indicator of energy reserves, was computed as the residuals from the regression of mass on body size (following Jakob et al. 1996). (2) Hematocrit, a widely used serological test to assess a bird's health status that evaluates the percentage of blood composed of red blood cells (Bush 1975, Svensson and Merila 1996), was measured following Campbell (1988). (3) Ectoparasite load (philopterid feather lice, identified using the method described in Price et al. 2003), was estimated by counting the number of louse eggs laid within the black feathers of the chest badge (rated on a 0–5 point scale). (4) Growth bar distance, an indicator of energy reserves at the time of molt (Grubb 1991), was calculated by measuring the distance between 5 and 7 bars on the blue region of the flag (following Grubb 1989). (5) Fluctuating asymmetry, which indicates developmental homeostasis (Van Valen 1962, Møller 1990), was measured as the absolute value of the difference in length of the two central rectrices. Body size was not correlated with tail asymmetry and, thus, did not bias measurements (male: $F = 0.43$, $df = 1$ and 46 , $P = 0.51$; female: $F = 0.05$, $df = 1$ and 50 , $P = 0.82$).

Assortative mating: General methods.—Mating patterns were studied at four large colonies. Pairs were identified by behavioral observations. Observations were conducted with spotting scopes from within a permanent blind located 45–55 m from each colony. Because some male–female associations were unstable during the long three-month prebreeding season, I analyzed assortative mating among birds that initiated a clutch together.

To assess the similarity of individuals to their mates, I compared three categories of measures for each male and female: (1) seven tail components, (2) body-size index (PC1), and (3) five measures of phenotypic condition. To control for potential effects of tail-feather loss on mating patterns and phenotypic condition, I excluded cases where one or both members of the pair lost both central tail feathers before clutch initiation.

Assortative mating (1): Within all pairs within study population.—In 2002, I examined the similarity of individuals to their mates within all pairs in the study population. I first analyzed data from pairs of all age classes ($n = 60$ pairs). To control for assortative mating for age class, I separately analyzed pairs composed of adults ($n = 53$ pairs).

Assortative mating (2): Within newly formed pairs.—Using data from both 2001 and 2002, I examined the similarity of individuals to their mates within newly formed pairs (birds that had not previously bred together). I analyzed pairs of all age classes ($n = 53$ pairs), and separately analyzed pairs composed of adults ($n = 45$ pairs).

Assortative mating (3): Within experimentally induced pairs.—Over a four-day period immediately before clutches were initiated, I removed 12 adult females from one colony and transported them ~100 km away. Females were removed from pairs that were stable for ≥ 30 days. After removal, all males successfully re-paired with females from the floater population. I compared tail components, body size, and phenotypic condition of males and females within the newly formed pairs (morphometric and condition data were available for 10 pairs).

Statistics.—Sexual dimorphism was analyzed with analyses of covariance (ANCOVA) for each tail component, with body size index (PC1) as a covariate to control for sexual differences in body size. Correlations among tail components, and between body size and tail components, were analyzed with pairwise correlation analysis. I used analysis of variance (ANOVA) to analyze sexual differences in body size. Repeated-measures ANOVA was used to analyze changes in tail components and body size between years. Because data from many years were combined, year was placed in the model to control for potential non-age-related differences in tail expression between years.

The analyses on assortative mating within all pairs and within newly formed pairs were conducted by correlating measures (seven measures of tail components, body size, and five measures of phenotypic condition) within pairs using pairwise correlation analysis. For the female-removal experiment, assortative mating was analyzed by ranking measures (tail components, body size, and phenotypic condition) within a sex and then comparing the rank of males and females within pairs using Spearman rank correlation.

Sequential Bonferroni corrections (Holm 1979) were applied to all analyses where multiple tests were applied to the same data set, and corrections were applied separately for the sexes. Sample

sizes for analyses are limited to pairs for which I had morphological or phenotypic condition measurements for both the male and female. All statistical analyses were two-tailed, and rejection level was set at $P > 0.05$. Descriptive statistics are listed as mean \pm standard error. Statistical power was evaluated for analyses that failed to reject the null hypothesis (Cohen 1988). Measurements of fluctuating asymmetry were log transformed to fulfill assumptions of normality.

RESULTS

Morphology.—Males were significantly larger (PC1) than females. The sexual dimorphism index (SDI) (computed as mean male / mean female) for tail components covered a large range (SDI: 1.0–1.10), with wire representing the most dimorphic tail component. After controlling for the sexual difference in body size, most tail components were significantly larger in males (Table 1).

Body-size characters were expressed with little variation (CV = 1.8–3.6), whereas variation in tail components covered a broad range (CV = 3.1–10.2). Wire was the most variable tail component in both sexes and was significantly more variable than body-size measures ($P \leq 0.001$ in all analyses; Table 1). Many tail components were intercorrelated in males and females. Body size was significantly correlated with most male tail components, but with few female tail components (Table 2).

Between the first (yearling) and second years of life, there was a significant increase in the size of most tail components and in traits used to characterize body size of males and females (Table 3). Between the second and third years of life, there were no significant changes in male or female tail components or measures of body size (with the exception of male bill length) (Table 4).

Assortative mating (1): Within all pairs in study population.—Among individuals of all ages, there were no significant relationships between tail components of mated males and females ($P > 0.10$, $r^2 \leq 0.04$, $n = 59$ –60 in all analyses). However, there was a nonsignificant trend for paired birds to have a similar flag area and

TABLE 1. Sexual dimorphism in mass, body size, and tail components of adult Turquoise-browed Motmots.

Morphology	Male		Female		Sexual difference			
	Mean (n)	CV	Mean (n)	CV	SDI ^a (m/f)	F^b	P	Significance ^c
Mass (g)	67.6 (147)	5.2	66.0 (104)	3.2	1.02	14.35	0.0002	*
Tarsus (mm)	23.3 (146)	2.8	23.2 (122)	2.6	1.00	2.99	0.08	NS
Bill (mm)	33.5 (146)	3.6	32.8 (122)	3.6	1.02	23.92	<0.0001	*
Wing (mm)	122.6 (147)	2.1	121.7 (122)	1.8	1.01	8.20	0.0045	*
Body size (PC1)	0.58 (144)		−0.04 (118)			19.42	<0.0001	*
Total tail (mm)	213.9 (146)	3.4	207.8 (117)	3.2	1.03	32.13	<0.0001	*
Racket (mm)	109.1 (140)	5.2	103.6 (115)	4.7	1.05	74.12	<0.0001	*
Base (mm)	105.4 (142)	3.6	105.8 (117)	3.1	1.00	3.93	0.05	NS
Wire (mm)	52.1 (140)	10.1	47.4 (116)	9.6	1.10	39.94	<0.0001	*
Blue of flag (mm)	30.5 (140)	7.7	28.9 (112)	8.8	1.06	21.00	<0.0001	*
Black of flag (mm)	26.5 (140)	7.2	26.3 (112)	7.4	1.01	0.07	0.80	NS
Flag area (cm ²)	14.7 (135)	9.9	13.8 (112)	9.2	1.07	18.74	<0.0001	*

^aSexual dimorphism index was computed as SDI = mean male/mean female.

^bBody size (PC1) was included as a covariate in analyses of sexual dimorphism of tail components.

^cSignificance indicated (* or NS) after sequential Bonferroni correction, applied separately to analyses of body size and tail components.

TABLE 2. Product moment correlations among and between tail components and body size (PC1). An asterisk indicates significant correlation after sequential Bonferroni correction, applied separately to analyses of males and females. Sample sizes are given in Table 1.

	Male						
	Total tail	Racket	Base	Wire	Blue of flag	Black of flag	Flag area
Total tail	1						
Racket	0.87*	1					
Base	0.68*	0.24*	1				
Wire	0.70*	0.87*	0.09	1			
Blue of flag	0.17	0.16	0.15	-0.21	1		
Black of flag	0.25*	0.17	0.23	-0.11	-0.15	1	
Flag area	0.26*	0.19	0.22	-0.22	0.53*	0.58*	1
Body size (PC1)	0.47*	0.38*	0.33*	0.30*	0.02	0.22*	0.19*

	Female						
	Total tail	Racket	Base	Wire	Blue of flag	Black of flag	Flag area
Total tail	1						
Racket	0.87*	1					
Base	0.71*	0.28*	1				
Wire	0.66*	0.85*	0.08	1			
Blue of flag	0.27*	0.25	0.20	-0.16	1		
Black of flag	0.24*	0.17	0.23	-0.06	-0.34*	1	
Flag area	0.42*	0.29*	0.39*	-0.12	0.46*	0.40*	1
Body size (PC1)	0.27*	0.20	0.23	0.10	0.09	0.14	0.16

body size (flag area: $F = 6.64$, $df = 1$ and 55 , $P = 0.01$, $r^2 = 0.11$, nonsignificant after sequential Bonferroni correction; body-size: $F = 3.50$, $df = 1$ and 58 , $P = 0.07$, $r^2 = 0.06$). There were no significant relationships between phenotypic condition of paired birds ($P > 0.10$, $r^2 \leq 0.04$, $n = 52-53$ in all analyses). However, there was a nonsignificant trend for paired birds to have similar ectoparasite loads ($F = 5.97$, $df = 1$ and 58 , $P = 0.02$, $r^2 = 0.09$, nonsignificant after sequential Bonferroni correction).

These patterns disappeared when yearlings were excluded from the analyses to control for age-assortative mating: tail components ($P > 0.10$, $r^2 < 0.05$, $n = 49-53$ in all analyses), body

size (PC1) ($P = 0.16$, $r^2 = 0.04$, $n = 52$), or phenotypic condition ($P > 0.10$, $r^2 \leq 0.06$, $n = 46-54$ in all analyses). Thus, there was no evidence of assortative pairing among adults.

Assortative mating (2): Within newly formed pairs.—Among individuals of all ages, there were no significant relationships between tail components of mated males and females ($P > 0.10$, $r^2 \leq 0.04$, $n = 53$ in all analyses). However, there was a nonsignificant trend for paired birds to have a similarly sized flag area and a dissimilarly sized racket (flag area: $F = 4.01$, $df = 1$ and 29 , $P = 0.06$, $r^2 = 0.13$; racket: $F = 5.17$, $df = 1$ and 52 , $P = 0.03$, $r^2 = 0.09$, nonsignificant after sequential Bonferroni correction). There were

TABLE 3. Change in body size and tail components between the first year (yearling) and second year of life.

Morphology	Male Yearling to second year of life				Female Yearling to second year of life			
	Mean change (mm)	F (n)	P	Significance ^a	Mean change (mm)	F (n)	P	Significance ^a
Tarsus (mm)	-0.1	0.72 (22)	0.41	NS	0.0	0.16 (27)	0.70	NS
Bill (mm)	0.7	19.23 (23)	0.0003	*	0.3	4.60 (23)	0.04	NS
Wing (mm)	2.7	103.28 (23)	<0.0001	*	2.3	53.10 (23)	<0.0001	*
Total tail (mm)	4.4	33.92 (22)	<0.0001	*	5.3	45.99 (29)	<0.0001	*
Racket (mm)	2.6	22.75 (22)	<0.0001	*	2.7	13.52 (24)	0.0014	*
Base (mm)	2.2	10.59 (22)	0.0042	*	2.9	30.80 (25)	<0.0001	*
Wire (mm)	0.3	0.19 (22)	0.67	NS	1.3	1.73 (24)	0.20	NS
Blue of Flag (mm)	1.0	6.80 (19)	0.0190	*	0.1	0.05 (22)	0.83	NS
Black of Flag (mm)	1.2	7.51 (19)	0.0145	*	1.4	9.17 (22)	0.0069	*
Flag Area (cm ²)	2.7	37.64 (13)	<0.0001	*	2.3	100.39 (18)	<0.0001	*

^aSignificance indicated (* or NS) after sequential Bonferroni correction, applied separately to analyses of body size and tail components, and separately to analyses of males and females.

TABLE 4. Changes in body size and tail components among adults between the second and third years of life.

Morphology	Male Second year to third year of life				Female Second year to third year of life			
	Mean change (mm)	<i>F</i> (<i>n</i>)	<i>P</i>	Significance ^a	Mean change (mm)	<i>F</i> (<i>n</i>)	<i>P</i>	Significance ^a
Tarsus (mm)	0.1	0.01 (13)	0.96	NS	0.0	1.74 (16)	0.92	NS
Bill (mm)	0.4	11.00 (14)	0.0077	*	0.8	7.08 (16)	0.0186	NS
Wing (mm)	0.3	1.43 (14)	0.25	NS	0.5	0.52 (16)	0.48	NS
Total tail (mm)	1.1	0.99 (12)	0.34	NS	1.5	3.20 (14)	0.10	NS
Racket (mm)	1.2	1.25 (12)	0.29	NS	1.3	4.24 (13)	0.06	NS
Base (mm)	0.4	0.77 (12)	0.40	NS	0.1	0.13 (13)	0.72	NS
Wire (mm)	0.7	0.71 (12)	0.42	NS	0.2	2.96 (13)	0.11	NS
Blue of flag (mm)	1.1	4.12 (12)	0.07	NS	1.2	2.46 (14)	0.14	NS
Black of flag (mm)	-0.7	2.15 (12)	0.17	NS	-0.6	0.68 (14)	0.43	NS
Flag area (cm ²)	0.5	1.94 (11)	0.20	NS	0.5	1.54 (15)	0.24	NS

^aSignificance indicated (* or NS) after sequential Bonferroni correction, applied separately to analyses of body size and tail components, and separately to analyses of males and females.

no significant relationships within pairs for body size (PC1) ($P = 0.97$, $r^2 = 0.01$, $n = 52$) or phenotypic condition ($P > 0.10$, $r^2 \leq 0.05$, $n = 27-52$ in all analyses).

When yearlings were excluded from the analyses to control for age-assortative mating, there were no significant positive relationships between tail components within paired birds ($P > 0.10$, $r^2 \leq 0.07$, $n = 23-45$ in all analyses). However, there was a trend for paired birds to have a dissimilarly sized racket ($F = 6.18$, $df = 1$ and 44 , $P = 0.02$, $r^2 = 0.13$, nonsignificant after sequential Bonferroni correction). There were no significant relationships within pairs for body size (PC1) ($P = 0.68$, $r^2 = 0.01$, $n = 44$) or phenotypic condition ($P > 0.10$, $r^2 \leq 0.06$, $n = 21-44$ in all other analyses). Thus, among adults, there was no evidence for positive assortative pairing, but there was a trend for negative assortative pairing for racket.

Assortative mating (3): Within experimentally induced pairs.—All males whose partners were experimentally removed successfully paired with females from the floater population. There were no significant relationships between tail components ($P > 0.10$, $df = 8$, $r^2 \leq 0.22$), body size ($P = 0.63$, $df = 8$, $r^2 = 0.01$), or phenotypic condition ($P > 0.10$, $df = 8$, $r^2 \leq 0.30$) of the replacement female and the original male.

DISCUSSION

When both sexes maintain sexually selected traits, pairs are predicted to form assortatively for those traits (Amundsen and Pärn 2006). In contrast to this prediction, I found no evidence that Turquoise-browed Motmots mate assortatively for various components of the elaborate racketed tail, body size, or phenotypic condition.

Assortative mating can be difficult to detect because ornamental variation within any given pool of mates may not reflect variation among the whole population. For example, if the available males have shorter-than-average tails, and the available females have longer-than-average tails, the most ornamented of each sex may pair, but their ornaments would be dissimilar from one another. To avoid these confounds, which are inherent in studies

of population-wide patterns of assortative mating, researchers can increase detectability by restricting their sample to individuals that have competed within the same pool of mates.

To increase detectability in this study, I examined mating patterns among all birds in the population and also among newly formed pairs. The second analysis was especially relevant to this species because many motmots remain paired with the previous year's mate and, as a result, a large proportion of the population is not included in the pool of available mates each season (Murphy 2005). Consequently, the mating pool is restricted to individuals that were previously unpaired, were divorced, or whose mate had died. Because variation in tail plumage is likely restricted within this limited pool, my second analysis of newly formed pairs correctly focused on tail variation among individuals that were in direct competition for mates. However, there was no evidence that pairs form assortatively for tail components, body size, or phenotypic condition in either the population-wide sample or the sample restricted to newly formed pairs.

As a further step to increase detectability of assortative mating, I forced new pairs to form by experimentally removing females from stable adult pairs. After mate removal, all widower males successfully paired with females from the floater population. However, among this sample, there was no evidence that pairs formed assortatively.

I had sufficient power (80%) at $P = 0.05$ in the correlative analyses to detect an effect size (r) as small as 0.55–0.36 with my sample sizes ($n = 23-60$ pairs; Cohen 1988). Six other studies of assortative mating found larger effect sizes ($r = 0.43-0.70$) with smaller sample sizes ($n = 18-22$) than those used in my analyses (Andersson et al. 1998, Daunt et al. 2003, Jawor et al. 2003, MacDougall and Montgomerie 2003, Kraaijeveld et al. 2004, Safran and McGraw 2004). I thus had sufficient power to detect a smaller effect size than has been reported in these other studies. Furthermore, even though sample sizes were limited in the mate removal experiment, this manipulative approach represents an extremely powerful method for detecting mating patterns and should have yielded marginally significant results if assortative mating occurred. Given the relatively strong power afforded by

my large sample sizes in the correlative analyses, and the strength associated with the manipulative approach, it seems reasonable to argue that mating patterns of the motmot are not strongly related to tail plumage, body size, or phenotypic condition.

Although I did not detect statistically significant assortative mating, some nonsignificant trends arose when birds of all ages were included in the analyses. However, all trends for positive assortative mating disappeared when I excluded yearlings, which suggests that assortative mating for age-class, and not ornament-based competition, accounted for this pattern (Perrins and McCleery 1985, Marzluff and Balda 1988, Warkentin et al. 1992). This interpretation is supported by the observation that more than half of the pairs that included yearlings were composed of two yearlings, and that tail components and body size generally increase between the first and second years of life and do not increase thereafter. Interestingly, there was a nonsignificant trend for adult pairs to form in a disassortative manner for racket. This trend may represent a statistical artifact (type I error). However, examples of negative assortative pairing are rare in birds (see Partridge [1983] and Houtman and Falls [1994] for studies on color-morph preferences), so future research should investigate whether this negative trend is biologically relevant.

I did not assess genetic reproductive success of mated pairs; therefore, it is possible that both sexes seek extrapair copulations (EPCs) with the most ornamented individuals, thus leading to assortative mating “behind the scenes.” Indeed, females may seek EPCs from the most ornamented males; however, it seems improbable that males would also discriminate in choosing EPC partners (i.e., it is unlikely that males would pass up an opportunity for an EPC) because of low cost associated with male copulations (*sensu* Bateman 1948).

The lack of assortative mating suggests that mutual sexual selection does not maintain the elaborate tail plumage in male and female motmots (see Muma and Weatherhead 1989, Hill 1993, Cuervo et al. 1996, Wolf et al. 2004 for other studies that failed to support the mutual sexual selection hypothesis). These results are consistent with previous research on this species, which has supported the hypothesis that sexual selection maintains tail length in males but not in females (Murphy 2007c). Why, then, do females also maintain such elaborate plumage? One possibility is that elaborate female plumage is expressed as a nonfunctional byproduct of genetic correlation (Lande 1980). However, it is also possible that different forms of selection operate on the elaborate traits of the sexes (Heinsohn et al. 2005, LeBas 2006). Because the motmot’s tail is used in a behavioral display by males and females in the presence of predators, it is possible that the naturally selected pursuit-deterrent benefit associated with the display (Murphy 2006, 2007a) is sufficient to account for the maintenance of the long racketed tail in both sexes, and that sexual selection acts to maintain the slightly longer male tail (male wires are ~10% larger than female wires). If this interpretation is correct, both natural and sexual selection work in concert in this species to maintain elaborate monomorphic plumage. Future research on this species and other elaborate monomorphic species should consider the hypothesis that elaborate traits do not function as sexually selected signals, as is often assumed, but rather that natural selection, or a combination of natural and sexual selection, can favor elaborate traits in both sexes.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation (DDIG 0206584), American Museum of Natural History, American Ornithologists’ Union, Andrew Mellon Foundation, Animal Behavior Society, Cornell Laboratory of Ornithology, Explorers Club, Mario Enaudi Foundation, Sigma Xi, and the Western Bird Banding Association. S. T. Emlen, P. W. Sherman, E. Adkins-Regan, H. K. Reeve, and D. W. Winkler, the Cornell Behavioral Lunch Bunch, and the Wink-Lab provided useful comments throughout the study, and their suggestions greatly improved the manuscript. Two anonymous reviewers, B. Kramer, and A. Lindo provided helpful comments on the organization of the manuscript. S. E. Bush was very generous in helping to identify feather lice. I am especially thankful to all the field assistants who participated in the study: N. Murphy, M. Flores, I. Hau, T. Marfil, T. Poole-DiSalvo, W. Hsu, S. Names, L. Fondow, K. Cook, B. Clock, Z. Nelson, A. Rassweiler, C. Egan, V. Steen, E. Macchia, and J. Smith. I am also indebted to technical support while in Mexico, provided by B. MacKinnon de Montes, R. Migoya von Bertrab, M. Quijano Farjat, and M. J. Tabasco Contreras, the staff of Niños y Crías, and the staff of the Ria Largas Biosphere Reserve. This research was conducted under Cornell University’s Institutional Animal Care and Use Committee protocol 99-23-02.

LITERATURE CITED

- AMUNDSEN, T. 2000a. Female ornaments: Genetically correlated or sexually selected? Pages 133–154 in *Animal Signals: Signaling and Signal Design in Animal Communication* (Y. Espmark, T. Amundsen, and G. Rosenqvist, Eds.). Tapir Academic Press, Trondheim, Norway.
- AMUNDSEN, T. 2000b. Why are female birds ornamented? *Trends in Ecology and Evolution* 15:149–155.
- AMUNDSEN, T., AND H. PÄRN. 2006. Female coloration: Review of functional and nonfunctional hypotheses. Pages 280–345 in *Bird Coloration: Function and Evolution*, vol. 2 (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey.
- ANDERSSON, S., J. ÖRNBORG, AND M. ANDERSSON. 1998. Ultra-violet sexual dimorphism and assortative mating in Blue Tits. *Proceedings of the Royal Society of London, Series B* 265:445–450.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- BEEBE, W. H. 1910. Racket formation in the tail-feathers of the motmots. *Zoologica* 1:140–149.
- BLANCO, G., J. DE LA PUENTE, M. CORROTO, A. BAZ, AND J. COLÁS. 2001. Condition-dependent immune defence in the Magpie: How important is ectoparasitism? *Biological Journal of the Linnean Society* 72:279–286.
- BOLAND, C. R. J., M. C. DOUBLE, AND G. B. BAKER. 2004. Assortative mating by tail streamer length in Red-tailed Tropicbirds *Phaethon rubricauda* breeding in the Coral Sea. *Ibis* 146:687–690.

- BURLEY, N. 1983. The meaning of assortative mating. *Ethology and Sociobiology* 4:191–203.
- BURLEY, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist* 127:415–445.
- BUSH, B. M. 1975. *Veterinary Laboratory Manual*. Heimann, London.
- CAMPBELL, T. W. 1988. *Avian Hematology and Cytology*. Iowa State University Press, Ames.
- CLAYTON, D. H., P. L. M. LEE, D. M. TOMPKINS, AND E. D. BRODIE III. 1999. Reciprocal natural selection on host–parasite phenotypes. *American Naturalist* 154:261–270.
- CLUTTON-BROCK, T. H., AND A. C. J. VINCENT. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* 351:58–60.
- COHEN, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd ed. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- CREIGHTON, E. 2001. Mate acquisition in the European Blackbird and its implications for sexual strategies. *Ethology, Ecology and Evolution* 13:247–260.
- CUERVO, J. J., F. DE LOPE, AND A. P. MØLLER. 1996. The function of long tails in female Barn Swallows (*Hirundo rustica*): An experimental study. *Behavioral Ecology* 7:132–136.
- DARWIN, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- DAUNT, F., P. MONAGHAN, S. WANLESS, AND M. P. HARRIS. 2003. Sexual ornament size and breeding performance in female and male European Shags *Phalacrocorax aristotelis*. *Ibis* 145:54–60.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- GRUBB, T. C., JR. 1989. Ptilochronology: Feather growth bars as indicators of nutritional status. *Auk* 106:314–320.
- GRUBB, T. C., JR. 1991. A deficient diet narrows growth bars on induced feathers. *Auk* 108:725–727.
- HEINSOHN, R., S. LEGGE, AND J. A. ENDLER. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science* 309:617–619.
- HILL, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the House Finch. *Evolution* 47:1515–1525.
- HOLM, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- HOUTMAN, A. M., AND J. B. FALLS. 1994. Negative assortative mating in the White-throated Sparrow *Zonotrichia albicollis*: The role of mate choice and intra-sexual competition. *Animal Behaviour* 48:377–383.
- JAKOB, E. M., S. D. MARSHALL, AND G. W. UETZ. 1996. Estimating fitness: A comparison of body condition indices. *Oikos* 77:61–67.
- JAWOR, J. M., S. U. LINVILLE, S. M. BEALL, AND R. BREITWISCH. 2003. Assortative mating by multiple ornaments in Northern Cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* 14:515–520.
- JOHNSTONE, R. A. 1997. The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology* 40:51–59.
- JOHNSTONE, R. A., J. D. REYNOLDS, AND J. C. DEUTSCH. 1996. Mutual mate choice and sex differences in choosiness. *Evolution* 50:1382–1391.
- JONES, I. L., AND F. M. HUNTER. 1993. Mutual sexual selection in a monogamous seabird. *Nature* 362:238–239.
- KRAAIJEVELD, K., J. GREGURKE, C. HALL, J. KOMDEUR, AND R. A. MULDER. 2004. Mutual ornamentation, sexual selection, and social dominance in the Black Swan. *Behavioral Ecology* 15:380–389.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305.
- LEBAS, N. R. 2006. Female finery is not for males. *Trends in Ecology and Evolution* 21:170–173.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116–121.
- MACDOUGALL, A. K., AND R. MONTGOMERIE. 2003. Assortative mating by carotenoid-based plumage colour: A quality indicator in American Goldfinches, *Carduelis tristis*. *Naturwissenschaften* 90:464–467.
- MARZLUFF, J. M., AND R. P. BALDA. 1988. Pairing patterns and fitness in a free-ranging population of Pinyon Jays: What do they reveal about mate choice? *Condor* 90:201–213.
- MASELLO, J. E., AND P. QUILLFELDT. 2003. Body size, body condition and ornamental feathers of burrowing parrots: Variation between years and sexes, assortative mating and influences on breeding success. *Emu* 103:149–161.
- MASSARO, M., L. S. DAVIS, AND J. T. DARBY. 2003. Carotenoid-derived ornaments reflect parental quality in male and female Yellow-eyed Penguins (*Megadyptes antipodes*). *Behavioral Ecology and Sociobiology* 55:169–175.
- MØLLER, A. P. 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour* 40:1185–1187.
- MØLLER, A. P. 1993. Sexual selection in the Barn Swallow *Hirundo rustica*. III. Female tail ornaments. *Evolution* 47:417–431.
- MUMA, K. E., AND P. J. WEATHERHEAD. 1989. Male traits expressed in females: Direct or indirect sexual selection? *Behavioral Ecology and Sociobiology* 25:23–31.
- MURPHY, T. G. 2005. Adaptive significance of elaborate plumage when expressed in both sexes: Multiple functions of the racketed-tail of the Turquoise-browed Motmot (*Eumomota superciliosa*). Ph.D. dissertation, Cornell University, Ithaca, New York.
- MURPHY, T. G. 2006. Predator-elicited visual signal: Why the Turquoise-browed Motmot wag-displays its racketed tail. *Behavioral Ecology* 17:547–553.
- MURPHY, T. G. 2007a. Dishonest ‘preemptive’ pursuit-deterrent signal? Why the Turquoise-browed Motmot wags its tail before feeding nestlings. *Animal Behaviour* 73:965–970.
- MURPHY, T. G. 2007b. Lack of melanized keratin and barbs that fall off: How the racketed tail of the Turquoise-browed Motmot *Eumomota superciliosa* is formed. *Journal of Avian Biology* 38:139–143.
- MURPHY, T. G. 2007c. Racketed tail of the male and female Turquoise-browed Motmot: Male but not female tail length correlates with pairing success, performance, and reproductive success. *Behavioral Ecology and Sociobiology* 61:911–918.

- OREJUELA, J. E. 1977. Comparative biology of Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. *Living Bird* 16:193–208.
- PARTRIDGE, L. 1983. Non-random mating and offspring fitness. Pages 227–255 *in* *Mate choice* (P. Bateson, Ed.). Cambridge University Press, Cambridge, United Kingdom.
- PERRINS, C. M., AND R. MCCLEERY. 1985. The effects of age and pair bond on the breeding success of Great Tits, *Parus major*. *Ibis* 127:306–315.
- PRICE, R. D., R. A. HELLENTAL, R. L. PALMA, K. P. JOHNSON, AND D. H. CLAYTON. 2003. The Chewing Lice: World Checklist and Biological Overview. Illinois Natural History Survey, Champaign.
- REGOSIN, J. V., AND S. PRUETT-JONES. 2001. Sexual selection and tail-length dimorphism in Scissor-tailed Flycatchers. *Auk* 118:167–175.
- SAFRAN, R. J., AND K. J. MCGRAW. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American Barn Swallows. *Behavioral Ecology* 15:455–461.
- SCOTT, P. E., AND R. F. MARTIN. 1983. Reproduction of the Turquoise-browed Motmot at archaeological ruins in Yucatán. *Biotropica* 15:8–14.
- SVENSSON, E., AND J. MERILÄ. 1996. Molt and migratory condition in Blue Tits: A serological study. *Condor* 98:825–831.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* *Sexual Selection and the Descent of Man, 1871–1971* (B. Campbell, Ed.). Aldine, Chicago, Illinois.
- VAN VALEN, L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125–142.
- WAGNER, H. O. 1950. Observations on the racquet-tips of the motmot's tail. *Auk* 67:387–389.
- WARKENTIN, I. G., P. C. JAMES, AND L. W. OLIPHANT. 1992. Assortative mating in urban-breeding Merlins. *Condor* 94:418–426.
- WOLF, W. L., J. M. CASTO, V. NOLAN, JR., AND E. D. KETTERSON. 2004. Female ornamentation and male mate choice in Dark-eyed Juncos. *Animal Behaviour* 67:93–102.

Associate Editor: M. T. Murphy