

FUNCTION OF TAIL STREAMERS OF RED-TAILED TROPICBIRDS (*PHAETHON RUBRICAUDA*) AS INFERRED FROM PATTERNS OF VARIATION

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ABSTRACT.—We investigated the function of Red-tailed Tropicbird (*Phaethon rubricauda*) tail streamers by quantifying patterns of variation in streamers and other measurable traits on the basis of measurements of 659 individuals, including 422 of known age and 459 of known sex, measured in the field from 2000 to 2002. Our data were consistent with the idea that Red-tailed Tropicbirds' tail streamer ornaments function for mate attraction, but it suggested that variability in streamer expression is arbitrary and unlikely to provide a meaningful signal of individual quality during mate choice. The two elongated red tail streamers are composed of bilaterally symmetrical filamentous central rectrices with a black rachis and narrow red vane averaging 399 ± 1.8 mm (SE) in length when fully grown. Prior to breeding, individuals of opposite sex conspicuously display elongated red tail streamers during complex aerial courtship. Streamers exhibited measurement asymmetries (the difference between new and old fully grown tail streamers) of up to 144 mm because of wear at the tip of the older streamer, which accounts for most of the difference in the lengths of two fully grown streamers in individual birds. As in other putative sexually selected traits, tail streamers were more variable than non-ornamental traits across individuals. Males were slightly larger than females in length of fully grown streamers (ratio 1.04), culmen length (ratio 1.02), and tarsal length (ratio 1.01). There was no correlation between fully grown streamer length and body size (score on first principal component) ($r = 0.004$), wing length (males, $r = 0.05$; females, $r = 0.10$), or mass (males, $r = 0.10$; females, $r = 0.04$), which is consistent with the hypothesis that streamers have an ornamental rather than aerodynamic function. There was a significant correlation between the ratio of streamer lengths (growing vs. fully grown, $r = 0.50$) of male and female pair members, indicating that at least the timing of ornament development was coordinated within pairs. However, tail streamers did not appear to be good indicators of an individual's "quality;" on the basis of 372 adults of known age (3–22 years), streamer length did not increase with age ($r = 0.30$) and was not correlated with an index of body condition ($r = 0.03$). The streamer length of pair members was not correlated with chick asymptotic body mass or chick fate, nor was female streamer length with egg size. Received 16 July 2002, accepted 24 July 2003.

RESUMEN.—En este estudio investigamos la función de las muy elongadas rectrices centrales de *Phaethon rubricauda* basándonos en los patrones de variación en las rectrices y otros caracteres medidos en el campo entre 2000 y 2002 en 659 individuos (incluyendo 422 de edad conocida y 459 de sexo conocido). Nuestros datos son consistentes con la idea de que los ornamentos de la cola de *P. rubricauda* funcionan para la atracción de pareja, pero sugieren que la variabilidad en la expresión de las rectrices es arbitraria y es poco probable que represente una señal significativa de la calidad de los individuos durante la selección de parejas. Las dos rectrices rojas elongadas están compuestas por plumas centrales filamentosas simétricas con ráquis negro y una vena roja estrecha que mide en promedio 399 ± 1.8 mm (EE) cuando está completamente crecida. Antes de la reproducción, durante el complejo cortejo aéreo, los individuos de sexos opuestos hacen despliegues conspicuos de sus rectrices. Las rectrices mostraron asimetría en las mediciones (diferencias entre rectrices nuevas y viejas completamente crecidas) de hasta 144 mm debido al desgaste de la punta de la más vieja, lo que representa la mayor parte de la diferencia entre las longitudes de dos rectrices completamente desarrolladas en un individuo. Como en otros caracteres presumiblemente seleccionados sexualmente, las rectrices centrales elongadas fueron más variables entre individuos que caracteres no ornamentales. Las longitudes de las rectrices completamente desarrolladas, del culmen y del tarso fueron ligeramente mayores en los machos que en las hembras (cociente 1.04, 1.02 y 1.01, respectivamente). No existieron correlaciones entre la longitud de las rectrices completamente crecidas y el tamaño corporal (valor en el eje del

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primer componente principal) ($r = 0.004$), la longitud del ala (machos, $r = 0.05$; hembras, $r = 0.10$), ni la masa corporal (machos, $r = 0.10$; hembras, $r = 0.04$). Esto es consistente con la hipótesis de que las rectrices elongadas tienen una función ornamental y no aerodinámica. Hubo una correlación significativa entre el cociente de longitudes de las rectrices (en crecimiento vs. completamente desarrolladas, $r = 0.50$) de los miembros macho y hembra de las parejas, indicando por lo menos un ajuste temporal en el desarrollo de los ornamentos en cada pareja. Sin embargo, las rectrices elongadas no parecieron ser buenas indicadoras de la "calidad" de los individuos: sobre la base de 372 adultos de edad conocida (3–22 años), la longitud de las rectrices no aumentó con la edad ($r = 0.30$) y no se correlacionó con un índice de condición corporal ($r = 0.03$). La longitud de las rectrices de los miembros de una pareja no estuvo correlacionada con el peso corporal asintótico de los pichones ni con la suerte de éstos. La longitud de las rectrices de las hembras no se correlacionó con el tamaño de los huevos.

ORNAMENTAL TRAITS SUCH as long tails, bright colors, forehead crests, and facial plumes displayed by birds during the breeding season may vary in expression between males and females, across age classes, and among individuals in ways that reveal much about their function (Andersson 1994). In many sexually dimorphic bird species (e.g. Long-tailed Widowbird [*Euplectes progne*], Andersson 1982; Barn Swallow [*Hirundo rustica*], Møller and Høglund 1988; Jackson's Widowbird [*Euplectes jacksoni*], Andersson 1992; and Shaft-tailed Whydah [*Vidua regia*], Barnard 1990), experimental evidence has demonstrated that male tail ornaments are favored by sexual selection because females prefer to mate with males with the longest and most elaborate tails. For example, in the Long-tailed Widowbird, Andersson (1982) lengthened male's tails by 20–30 cm and found males with elongated tails were more successful (higher mean number of nests per male) than males with shortened or control tails. Females preferred males with supernormal tails—elongated males had highest success (Andersson 1994). Such sexually selected ornamental traits exhibit high levels of variation compared with traits thought to be because of other forms of natural selection (Alatalo et al. 1988, Jones and Montgomerie 1992, Evans and Barnard 1995, Jones et al. 2000). That variation has been suggested to result from lack of stabilizing selection on those ornamental traits (Alatalo et al. 1988) or the tendency for ornaments to be costly and sometimes correlated with an individual's health (e.g. Møller 1991). In some polygynous birds, there is male-biased sexual dimorphism and high variability of male ornaments (e.g. Petrie et al. 1991); whereas in monogamous species, males and females (sexes monomorphic) may have similar ornaments that are favored by mutual sexual selection (Jones and Hunter

1993, 1999). Recent experimental studies provide strong evidence that female ornamentation is not severely constrained by selection on males and has evolved independently of male showiness (Amundsen 2000). Few studies (e.g. Hill et al. 1999, Witte and Curio 1999, Jones et al. 2000) have investigated ornament variation in a monogamous sexually monomorphic bird species.

Tropicbirds (Pelecaniformes, Phaethontidae) include three sexually monomorphic, socially monogamous tropical seabird species, all of which have conspicuous tail streamers. The adult Red-tailed Tropicbird (*Phaethon rubricauda*) is pigeon-sized with satin-textured white plumage, a red-orange bill, and two flexible elongated red central feathers that form conspicuous tail streamers a body length long. Males and females perform complex aerial courtship displays prior to breeding. Groups of vocalizing tropicbirds circle about in the sky above the breeding area; a pair (or sometimes trio) will separate from the group and begin synchronized flight maneuvers in which one bird hovers above the other, the upper bird is carried backward by the wind, it then glides forward in a downward curve and the lower bird begins a hover-backward rise. Both birds slowly twitch their streamers from side to side. The result is alternating vertical circles (Fleet 1974, Schreiber and Schreiber 1993, A. C. Veit and I. L. Jones pers. obs). That scene presents a biologist with an improbable sight. What is the function of the red streamers, and what mechanism could possibly explain their evolution? Use of streamers in those displays, together with the finding that adults' brief possession of two fully grown streamers coincides with their prelaying period (A. C. Veit and I. L. Jones unpubl. manuscript), strongly suggests a sexually selected function for tail streamers. The

slender lifting-surface theory suggested that only the part of the tail proximal to the point of maximum continuous width is aerodynamically functional and the tail behind that point is relatively free from aerodynamic-selection pressures (Thomas 1993). Because tail streamers extend far beyond the point of maximum width of the rest of the tail, aerodynamic theory indicates they generate drag but no lift, which suggests that they are unlikely to enhance flight performance (Balmford et al. 1993, Thomas 1993). Tail streamer ornaments formed by elongated central rectrices (pin tails) may have no beneficial aerodynamic function but instead have arisen as sexually selected ornaments that function to attract mates or in intrasexual competition (Balmford et al. 1993, Thomas 1993). Allowing for the possibility that the streamers might have some function related to flight, as yet unexplained by aerodynamic research, we looked for an allometric relationship between tail streamer length and body size (PC1), wing length, and body mass. We predicted that if Red-tailed Tropicbird tail streamers have a significant flight function, they should correlate across individuals with other aerodynamically important traits such as wing length.

Here, we quantified variation in tail streamer ornaments of the Red-tailed Tropicbird to assess the role of sexual selection in tropicbird ornament evolution and for comparison with other studies of sexually selected ornaments. To assess ornaments' roles as signals of viability, we attempted to estimate (1) effects of age and year on ornamental expression, and (2) relations of ornament size to body condition and breeding performance. Finally, we investigated assortative mating related to ornaments. Because of the active nature of tropicbird flight displays and the logistical difficulties encountered when attempting to follow marked individuals, intensive behavioral observations and quantification data were not collected.

We evaluated our findings in relation to two independent hypotheses concerning streamer function: (1) streamer function is mainly aerodynamic and enhances flight performance, and (2) streamer function is mainly ornamental and favored by inter- or intrasexual selection. Within hypothesis (2), we considered two alternatives: (i) streamers are condition-dependent indicators of individual quality (i.e. a "good genes" or "handicap" process; Andersson 1986,

Pomiankowski 1988); and (ii) streamer expression is arbitrary because they are the product of a sexual selection mechanism not involving condition-dependence (i.e. a runaway process, Fisher 1930; Kirkpatrick 1982; Lande 1980, 1981; or sensory exploitation, Ryan and Rand 1993).

METHODS

Fieldwork was carried out at a colony of >600 breeding pairs of Red-tailed Tropicbirds at Tern Island, French Frigate Shoals in the Northwestern Hawaiian Islands (23°45'N, 166°15'W), during early April to mid-August 2000, early February to mid-May 2001, and January–February 2002. Tropicbirds were captured by hand at nest sites under shrubs (*Tournefortia argentea*) or buildings along the south and north sides of Tern Island. Unbanded tropicbirds were banded with a numbered stainless steel leg band; band numbers of previously banded birds were recorded. A 0.3 mL blood sample was collected from the tarsal vein of the left leg with a 22.5 gauge sterile needle attached to a 1 mL syringe. The procedure took ~1 min. The blood sample was then transferred to a plastic vial containing a small amount of 100% ethanol for preservation and storage. Body mass was measured to the nearest 1 g using an electronic balance. Body mass^{1/3} was used to permit direct comparison of variation in body mass with variation in linear variables. The following linear measurements were taken: exposed culmen (from bill's tip to the tip of the feathering at the base of the bill), bill width (taken at the anterior end of nostrils), bill depth (taken even with the anterior end of nares), diagonal length of tarsus (on left leg, from midpoint of tibiotarsal joint to distal end of tarsometatarsal joint on underside of the foot), and (if bird was on nest) length and breadth of egg to the nearest 0.1 mm using stainless steel calipers. Left and right wing length (flattened and straightened) and total head length (from tip of bill to the occipital condyle) were measured to the nearest 1 mm using a 45 cm stainless steel wing ruler, and left and right streamer length (from insertion to tip, on ventral surface) were measured to the nearest 1 mm using a 60 cm stainless steel ruler. Bases of both streamers were inspected for evidence of molt and assigned a score of 1, 2, 3, 4, 5, or 0—a score of 1 indicated absent or in pin. Absent was defined as "no pinfeather present" (seen and felt). "In pin" referred to a pin feather within a sheath with no exposed feather vane. A score of 2, 3, and 4 indicated a growing (molting) streamer. A growing streamer had a whitish sheath remaining at the base and was scored by length: 2 (10 to 199 mm), 3 (200 to 299 mm), and 4 (300 mm to fully grown). A growing streamer was measured if it was at least 10 mm in length (feather exposed from sheath) through lengths >300 mm. A score of 5 indicated a new, fully grown and 0 indicated an old, fully grown

streamer (Ashmole 1962). New and old fully grown streamers were distinguished by color (bright red vs. faded) and wear (unworn vs. abraded at the tip). The states of color were not coded. Abrasion at the tip was defined by worn-away vane or abraded whitish-pink vane at the streamer tip. Two independent measures of wing and streamer lengths only (because of time limitations related to stress on the birds during handling) were taken to quantify measurement error and repeatability. Measurement error (ME), the proportion of within-individual variation to total variation was calculated as $ME = MS_{\text{within}} / (s^2_A + MS_{\text{within}}) \times 100\%$. Repeatability of measurements within measurer was defined as r_v , the intraclass correlation coefficient (Bailey and Byrnes 1990). Independent measures were achieved by measuring the left streamer, then the right streamer, removing the ruler and repositioning it at the left streamer for the second set of measurements. We recorded the status of nesting activity as not active, active with egg, or active with chick. Tail streamer measurements were collected on individuals without an active nest (just sitting on ground); however, those individuals were not identified as paired. Male and female tropicbirds are morphologically indistinguishable externally; therefore, sex was determined based on analyses of blood samples using the genetic sexing technique described by Fridolfsson and Ellegren (1999) or cloacal morphology near egg-laying (P. Sievert unpubl. data). Nests were checked daily, so the exact date of laying was known. Cloaca of one of the mates on the day of laying and cloaca of the other mate when it returned from sea (1–10 days later) were examined. The pair member with the most distended cloaca (raised or thickened, usually by ~2 mm more) was judged to be the female. The diagnostic character was thickening of the cloaca because the color and diameter did not vary consistently.

To determine the best measure for streamer size, it was necessary to consider molt and feather wear. In many species, ornamental rectrices develop simultaneously and completely prior to the breeding season; that is not the case in the Red-tailed Tropicbird. Tropicbird streamers molt alternately with each streamer taking about six months to complete growth; each streamer is then retained at full length for approximately six months thereafter (A. C. Veit and I. L. Jones unpubl. manuscript). Thus, when a tropicbird returns to its nesting island, it normally has two fully grown streamers, one recently fully grown and the other having been fully grown for about six months and showing signs of wear (A. C. Veit and I. L. Jones unpubl. manuscript). Length of one fully grown streamer (right or left side) was used to quantify an individual's ornament size. Only individuals with a fully grown streamer that showed no signs of wear at the tip or breakage along its length were included in the analysis.

To quantify variation in ornament expression, or-

naments of adult tropicbirds were compared among the years 2000–2002, on the basis of one set of measurements (at first capture) from each individual. Variation in ornament expression was also quantified between years in individuals that were measured in multiple years. To quantify directly age-related differences in ornaments, many of the birds measured ($n = 422$) had been banded as chicks and were of known age. To obtain a body size index, a principal components analysis (transformation method Orthotran/Varimax) was performed on individuals' raw wing, tarsus, and culmen lengths; the first principal component was used as the size variable (Table 1). Residuals of the regression of body mass on body size were used as an index of body condition for comparison with ornament expression. Allometric regressions were carried out for wing, culmen, and tarsus lengths, as well as body condition, using simple linear regression. Estimates of slopes, intercepts, and confidence intervals are provided.

To examine the relationship between ornament expression and breeding phenology, male and female pair members were identified and nests were monitored in years 2000 ($n = 59$) and 2001 ($n = 44$). The female lays a single egg. Each nest was checked every two days to record nesting-activity status and pair-member attendance. Dates of laying, hatching, and fledging for nests were recorded. Egg volume was calculated using the formula $0.512 \times (\text{egg length} \times 0.1) \times [(\text{egg width} \times 0.1)^2]$ (Birkhead and Nettleship 1984). No variation in egg shape was noticed that could have "muddled" the egg volume estimates. Egg-volume index was used to determine if female streamer length predicted egg size. Chick body mass was measured every seven days throughout the three-month chick-growth period using an electronic balance (to nearest gram). Asymptotic chick body mass at 58 days (mean time to asymptote) was used for analysis to explore the relationship between parent streamer length and body mass of its chick. Female and male ornament expression were examined to determine if they were influenced by body condition index in the previous year. Nest fate (egg failed, dead chick, or fledged chick) was examined to determine if it was influenced by ornament expression of parents. To examine the relationship between ornament expression of male and female pair members, fully grown streamer

TABLE 1. Principal component factor analysis for measures of body size of male and female Red-tailed Tropicbirds ($n = 124$).

	Unrotated factor 1
Eigen value	1.27
Percent variance	42.2
Length of wing	0.507
Length of culmen	0.748
Length of tarsus	0.670

lengths and the mean ratio of streamer lengths were compared. Ratios close to 1.0 represented two fully grown streamers or one fully grown streamer and one streamer almost fully grown; ratios <0.5 represented one fully grown streamer and one streamer beginning to grow. Pair members were measured within 10 days or less of each other and used only once in the analysis unless from different years.

RESULTS

Ornament measurement.—We captured and measured 241 male, 192 female, and 226 unknown sex individuals. Many birds were captured more than once in the same year, and some again in the next year. Retraps within years constituted 29% ($n = 349$) of captures and retraps between years 67% ($n = 807$) of captures for a total of 1,206 captures. Repeatability of measurements within measurer (r_1 , the intra-class correlation coefficient) was high (0.90–1.0); and measurement error (ME), the percentage of total variability because of within-individual variation (Bailey and Byrnes 1990), was very low (0.08–0.23%; Table 2). We noted measurement asymmetry of fully grown tail streamer (a difference between left and right fully grown tail streamers) on the basis of measurements of birds with two fully grown streamers (mean = 47.8 ± 3.5 mm [SE], range = 1.5–144.5 mm). Asymmetries were partly attributable to wear of the older streamer. We also noted measurement asymmetry of fully grown tail streamers from two consecutive years for the same bird

(length of fully grown left streamer from year [n] and fully grown right streamer from year [$n + 1$]) (mean = 27.2 ± 3.0 mm [SE], range = 0.5–141.0 mm). The mean wear rate of a fully grown streamer was 0.3 ± 0.03 mm (SE) day⁻¹ (A. C. Veit and I. L. Jones unpubl. manuscript).

Variation of ornament compared to other traits.—Fully grown tail streamers had higher coefficients of variation than nonornamental traits (Table 3). Fully grown tail streamer length (range = 190.0–524.0) was the most conspicuously variable trait whereas culmen (range = 56.3–68.2) and wing lengths (range = 305.2–340.0) were less variable. Standard error (SE) was calculated for coefficients of variation using $S_v = V/2\sqrt{n}$, where $V = 100s/Y$ (Sokal and Rohlf 1995). Allometric regressions of wing, culmen, and tarsus lengths, as well as body condition variables, were not statistically significant (Table 4).

Sexual dimorphism and ornament variability of males and females.—Patterns of variation were similar between the sexes (Table 3). Fully grown male tail streamers were 4% longer than mean female fully grown tail streamers. That difference was statistically significant at a tablewide level of 0.05. Otherwise, males were slightly larger in body size (PC1) than females (unpaired $t = 2.7$, $df = 122$, $P = 0.008$).

Ornament variation among years and with age.—Length of fully grown tail streamers varied significantly across years in females but not in males (females: ANOVA, $F = 5.1$, $df = 2$ and

TABLE 2. Measurement error and within-measurer repeatabilities of the Red-tailed Tropicbird ornament and wing measures.

Ornament	ME (%) ^a	r_1	SE	F	df	P
Tail streamer length	0.08	1.00	–	0.000	302	0.98
Wing length	0.23	0.90	–	0.001	241	0.97

^aME: measurement error, the proportion of within-individual variation to total variation, $ME = MS_{within}/(s^2_A + MS_{within}) \times 100\%$ (Bailey and Byrnes 1990).

TABLE 3. Variation of morphological traits and mass of adult male and female Red-tailed Tropicbirds.

Variable	Males		CV	Females		CV	SD ^a	t	df	P
	(Mean \pm SE)	n	(%)	(Mean \pm SE)	n	(%)	(m/f)			
Streamer (mm)	403.4 \pm 2.9	218	10.7	388.0 \pm 3.3	177	11.2	1.04	3.5	393	0.005 ^b
Wing (mm)	324.6 \pm 0.9	62	2.2	323.8 \pm 0.8	63	1.8	1.00	0.7	122	0.50
Culmen (mm)	62.4 \pm 0.3	62	3.6	61.3 \pm 0.3	63	3.5	1.02	2.8	123	0.005 ^b
Tarsus (mm)	28.2 \pm 0.2	61	4.3	27.9 \pm 0.2	63	4.6	1.01	1.1	121	0.30
Body mass ^{1/3} (g)	218.7 \pm 2.0	62	7.2	220.2 \pm 2.3	63	8.2	1.00	0.5	123	0.60

^aSD: Sexual dimorphism index (male trait size/female trait size).

^bSignificant differences at a tablewide $P < 0.05$, using sequential Bonferroni analysis.

TABLE 4. Allometric relationships of body size measures (mm) on fully grown streamer length (mm).

	Intercept (95% C.I.)	Slope (95% C.I.)	<i>n</i>	<i>r</i> ²	<i>P</i>
Wing (mm)	200.26 (-210.69, 611.2)	0.61 (-0.66, 1.88)	104	0.009	0.341
Culmen (mm)	483.64 (274.06, 693.22)	-1.38 (-4.76, 2.00)	104	0.006	0.421
Tarsus (mm)	343.16 (171.49, 514.83)	1.98 (-4.14, 8.09)	103	0.004	0.523
Condition index	398.61 (390.70, 406.54)	-0.28 (-8.47, 7.91)	103	0.000	0.947

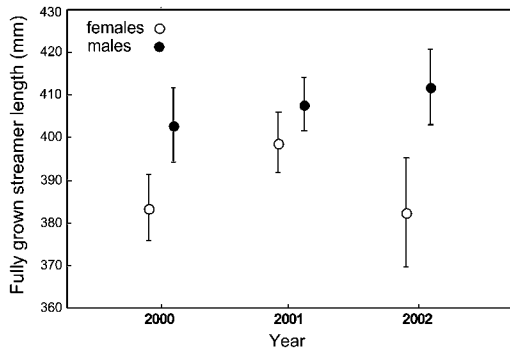


FIG. 1. Variation in male and female fully grown tail streamer expression according to year at Tern Island, 2000–2002 (means = 95% confidence limits).

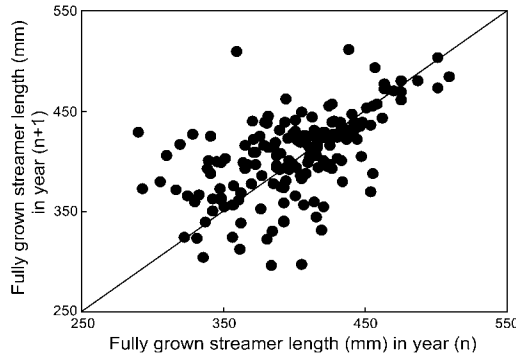


FIG. 2. Plot of fully grown streamer length at first capture in year (*n* + 1) versus length at first capture in year (*n*) of Red-tailed Tropicbirds, based on 172 individuals measured twice (line indicates 1:1, i.e. no change in ornament size).

279, *P* = 0.01; males ANOVA, *F* = 1.0, *df* = 2 and 352, *P* = 0.40; Fig. 1). For individuals that were measured in multiple years, fully grown tail streamers did not vary between years (ANOVA, *F* = 1.3, *df* = 1 and 105, *P* = 0.20). On the basis of 172 individuals with a fully grown streamer at initial capture in the first year and again with a new fully grown streamer at recapture in subsequent years, there was a strong correlation with high repeatability (*r* = 0.50, *P* < 0.0001, *r*₁ = 1.0; Fig. 2); but some evidence of a slight increase in streamer length between years (101 increased between years, 68 decreased between years, binomial *P* = 0.004, Fig. 2). However, on the basis of 372 of known age (3–22 years old, mean = 9.6 years), we found no correlation between the fully grown streamer length and age of individual (*r* = 0.30, *P* = 0.60; Fig. 3). There was no difference between males and females in the relationship between fully grown streamer length and age (ANCOVA, *F* = 1.3, *df* = 1 and 195, *P* = 0.30). Ornament expression did not increase with age.

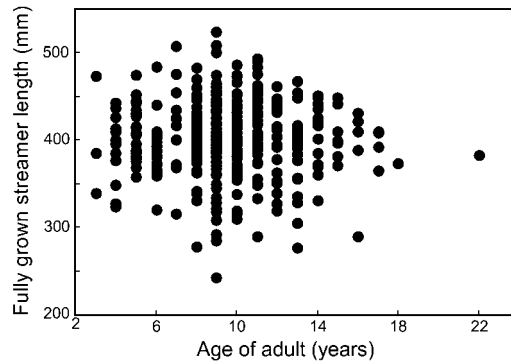


FIG. 3. Plot of fully grown streamer length versus age versus of Red-tailed Tropicbirds, based on 372 individuals.

Covariation with ornaments and other traits.—Fully grown tail streamer length was not correlated with body size (PC1) (*r* = 0.004, *df* = 102, *P* = 0.90), mass (*r* = 0.40, *df* = 103, *P* = 0.70), or wing length (*r* = 0.10, *df* = 103, *P* = 0.30).

There was no evidence for covariation of the tail streamer ornament with other morphological traits (culmen and tarsus) within individuals, except for a weak negative correlation between female streamer and culmen length (Table 5).

Relationship of ornament to condition and breeding performance.—Male and female fully grown tail streamer lengths were not correlated with condition index across individuals (*r* = 0.03, *df* = 102, *P* = 0.70). No relationship was

TABLE 5. Correlation matrix for adult male and female Red-tailed Tropicbird fully grown tail streamers and morphological traits (r for males above major diagonal and r for females below; $n = 50$ males and $n = 53$ females measured).

	Wing	Culmen	Tarsus	Streamer
Wing	1.00	0.081	0.090	0.009
Culmen	0.056	1.00	0.113	-0.042
Tarsus	0.091	0.265	1.00	0.211
Streamer	0.093	-0.273 ^a	-0.117	1.00

^aSignificant differences at a tablewide $P < 0.05$, using sequential Bonferroni analysis.

found between fully grown streamer length and body condition of the previous year (female: $r = 0.02$, $df = 44$, $P = 0.90$; male: $r = 0.10$, $df = 29$, $P = 0.50$) nor between the lay date of an individual and streamer length ($r = 0.10$, $df = 151$, $P = 0.50$). We found no correlation between egg volume index and female streamer length ($r = 0.002$, $df = 51$, $P = 1.0$). There was no difference in ornament expression between individuals with chicks that fledged and individuals with chicks that died before fledging (unpaired $t = 0.6$, $df = 71$, $P = 0.60$) nor with individuals with failed eggs before hatching (unpaired $t = 0.6$, $df = 49$, $P = 0.50$). Finally, we investigated the relationship between the fully grown streamer length of male and female pair members and the asymptotic body mass of their chick. No significant correlations were found (male: $r = 0.60$, $df = 8$, $P = 0.09$; female: $r = 0.30$, $df = 11$, $P = 0.30$).

Evidence for assortative mating.—No correlation was found between the fully grown tail streamer length of male and female pair members ($r = 0.20$, $df = 56$, $P = 0.30$). However, a correlation was found between the ratio of the lengths of the two streamers (growing streamer vs. fully grown streamer) of pair members ($r = 0.50$, $df = 35$, $P = 0.01$; Fig. 4), which suggests that individuals paired with mates with similar tail streamer symmetry as determined by stage of growth. Males and females tended to repair with each other. Of the original 59 pairs monitored in the first year, 41 of those paired with the same mate in the second year.

DISCUSSION

A Red-tailed Tropicbird flying high against a blue sky hundreds of miles from the nearest land with plumage mostly gleaming white, except for brilliant red central streamers trailing a body length or more behind, presents a

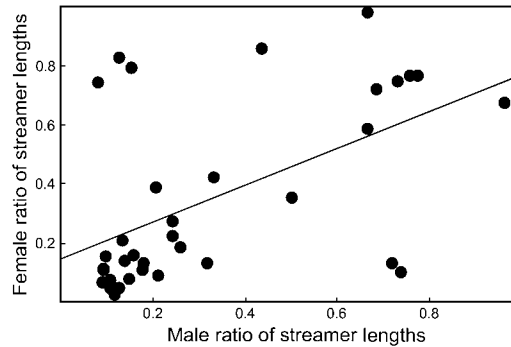


FIG. 4. Regression plot of male-pair member ratio of streamer lengths versus female-pair member ratio of streamer lengths in Red-tailed Tropicbirds. Ratios close to 1.0 are long growing streamers nearly fully grown, ratios < 0.5 are streamers beginning to grow. Pairs have streamers of similar symmetry.

biologist with an improbable sight. What are the awesome red streamers used for, and what mechanism could possibly explain their evolution? In common with other sexually selected traits, both male and female tail streamers were more variable (higher coefficients of variation) than nonornamental morphological traits such as culmen, wing, and tarsus lengths. Ornament expression was similar between sexes, except in streamer length, which was 4% longer in males. We do not believe that expression of tail streamer ornaments in tropicbird females is a simple result of genetic correlation between male and female traits (e.g. Lande and Arnold 1985) in which selection on one sex drags along a response in the other. In some monogamous species, as in the Long-tailed Skua (*Stercorarius longicaudus*), long tail ornaments have evolved in both sexes, which may signal breeding experience and parental ability (e.g. Andersson 1971, 1976). That idea predicts that long tail ornaments in both sexes should occur mainly in species with biparental care and that the degree of similarity of the tail in males and females should be correlated with the similarity of their parental roles (Trivers 1972, Andersson 1994). Parental care of Red-tailed Tropicbirds is shared equally by both parents, which supports the aforementioned prediction. Growing evidence suggests a role for mutual sexual selection favoring both male and female ornaments (Hill 1993; Jones and Hunter 1993, 1999; Amundsen et al. 1997) and mutual preferences for plumage color (Burley 1977, Burley and Moran 1979).

Males' greater ornament expression (Fig. 1) may be explained by stronger intersexual selection on the males ornamental trait, such as a stronger female preference for male tail length, or differences between males and females in ability to produce the ornament, or differences between sexes in costs of mate choice (Johnstone et al. 1996).

A significant correlation and high repeatability were found with individuals' tail streamer ornaments among years, indicating that streamers grow to a similar final length each year. Red-tailed Tropicbirds in possession of two fully grown tail streamers exhibited measurement asymmetries (the difference between left and right fully grown tail streamer) of up to 144 mm because of wear at the tip of the older streamer. That wear accounted for most of the difference in the lengths of two fully grown (one old, one new) streamers in individual birds. There was no evidence that ornament expression changed with age (3–22 years). That may indicate that Red-tailed Tropicbirds' streamer length may not be a good indicator of quality, at least as measured by individuals' age and experience. Andersson (1971, 1976) found that the two central tail streamers of the Long-tailed Skua used in courtship display by both sexes appeared to increase in length with age. Our results were more similar to those of previous studies on sexually monomorphic feather ornaments of Crested Auklet (*Aethia cristatella*) and Least Auklet (*A. pusilla*) (Jones and Montgomerie 1992, Jones et al. 2000), which are spectacular but cheap to produce and apparently arbitrary in expression, which in part suggested the ornaments might be unreliable viability indicators.

Streamer length, although highly variable across individuals, had no relationship with other structures important to flight such as body size (PC1), wing length, or mass among 103 individuals that were measured. If streamers were important to flight performance, we would expect them to be longer on larger, longer winged, and heavier individual birds; but there were no such relationships. Taken together with the aerodynamic theoretical prediction (that a streamer projecting beyond the point of maximum span of the tail will have no aerodynamic benefit, Thomas 1993), available evidence suggests that tropicbird tail streamer ornaments do not have a beneficial aerodynamic function.

Tail streamers consist of bright red carotenoid, melanin pigments, and structural keratin amounting to less than a gram on a bird averaging ~700 g in body mass. Their slender profile is unlikely to generate significant aerodynamic drag (Thomas 1993), so the energetic costs of streamer production and display of those ornaments might reasonably be assumed to be small. However, unlike all other bilaterally symmetrical avian feather ornaments, Red-tailed Tropicbird tail streamers are grown alternately (i.e. one at a time in sequence) and slowly (six months to produce each streamer; A. C. Veit and I. L. Jones unpubl. manuscript), consistent with their being (1) a costly trait that can only be developed over a long period or (2) a cheap trait that provides little benefit and thus has a low priority for growth. Nevertheless, we considered the hypothesis that the streamers might function as viability indicators used in mate choice. In some bird species, size of tail ornaments has been found to reflect condition (e.g. Møller 1989), which makes Red-tailed Tropicbird tail streamers a possible case of indicator function (Andersson 1982). However, we found no evidence that tail streamer ornaments were correlated with measures of individual viability. We found no correlation between ornament size and a mass-based body condition index, which suggests that Red-tailed Tropicbird tail streamer ornaments may not be strong signals of individual condition. The condition index was based on mass during incubation and chick-rearing periods of individuals captured haphazardly at or near their nest sites. Using mass may not be the most appropriate way to evaluate condition because of fluctuations in mass measurements throughout an individual's lengthy incubation shifts. Alternative methods to assess an individual's body condition should be considered, such as haematocrit, a method which is used to determine the volume of packed cells in the blood (Carpenter 1975). Saino et al. (1997) found hematocrit to be a useful measure of an individual's quality and found significant correlations with Barn Swallow ornaments.

There were no statistically significant correlations between streamer length and breeding performance as measured from timing of breeding, egg size, chick asymptotic body mass, and nest fate. In males, a positive trend was found between ornament size and chick body mass; but because of the small sample size, results must be interpreted cautiously. In a study by

Johnsen et al. (1996), female epaulet color in Red-winged Blackbirds (*Agelaius phoeniceus*) was influenced by female condition from the previous year. Testing for both males and females, we did not find that to be the case with tropicbirds; streamer length was not influenced by condition of the previous year. Data are more consistent with the hypothesis that the evolutionary origin of the tail streamer was a result of a runaway or sensory exploitation mechanism than a viability indicator mechanism.

There was some contradictory evidence related to assortative mating. First, we found no correlation between streamer lengths of male and female pair members ($n = 57$), which suggests that length of a fully grown streamer was not a sole determining factor in mate choice. We did find a correlation of the ratio of streamer lengths (growing streamer vs. fully grown streamer) between pair members measured within 10 days or less of each other, which indicates that timing of streamer molt was synchronized within pairs. It is in the best interest of an individual to have both tail streamers fully grown or nearly fully grown at the beginning of the breeding season for courtship displays signaling a readiness to breed. Those findings suggest that the symmetry of streamers is an important optical signal. If streamers act as signals of individual quality, the length of an elongated pintail may not be a particularly reliable indicator of heritable quality. Another cue, such as symmetry, might be required (see Møller 1992, 1993; but also Balmford and Thomas 1992). To confirm the role of sexual selection in favoring tropicbird ornaments, we require field experiments to assess the effect of manipulations of male and female streamer length on their mating success.

Taken together, our findings strongly suggest that tail streamer ornaments of Red-tailed Tropicbirds are a sexually selected trait, showing high levels of variability in expression similar to the costly sexually selected ornaments of other bird species (Alatalo et al. 1988). However, expression of the ornament seems to be arbitrary, and the tail streamer ornament does not appear to be a good indicator of an individual's quality. To date, there is no experimental evidence to show if mutual sexual selection by mate choice may favor similar tail streamer ornaments in both males and females of the Red-tailed Tropicbird. More research is required to further clarify the function of the tail streamer

ornament, for example: (1) to observe courtship displays and interactions to determine behavioral roles of sexes; (2) to investigate other factors responsible for ornament variability; (3) to investigate the aerodynamic implications and explain the unusual alternating molt pattern of tail streamers; (4) to experimentally manipulate tail streamer length and symmetry of marked individuals to confirm the role of the ornament in determining mating success; and (5) to investigate the function of other display traits (i.e. soft parts, plumage, and vocalizations) and communicative behavior.

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