

Short communication

Timing and patterns of growth of Red-tailed Tropicbird *Phaethon rubricauda* tail streamer ornaments

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The tail streamers, forehead crests and facial plumes displayed by some birds are unusual, sometimes spectacular, structures that vary in expression between the sexes, with age and among individuals (Andersson 1994). An unusual example of avian ornamentation is the elongated pin- or streamer-tails displayed by tropicbirds (Pelecaniformes, Phaethonidae). Such ornaments formed by elongated central rectrices are thought to be the product of sexual selection because they may have no clear aerodynamic function but instead serve as optical display structures used during the breeding season for the purposes of mate attraction and intrasexual competition (Balmford *et al.* 1993). Adult tropicbirds have 14 rectrices, including the two central streamers (Gould *et al.* 1974, Del Hoyo *et al.* 1992). The moult of tropicbird tail streamers has not been quantified rigorously (Schreiber & Schreiber 1993, Lee & Walsh-McGehee 1998). Because the timing of development of ornamental feathers in relation to the timing of the breeding season is crucial for understanding their function, it is essential to elucidate patterns of moult, including the loss of old feathers and the growth of new ones (Ginn & Melville 1983). Therefore, we quantified tail streamer moult in relation to the timing of breeding, age and sex of individuals.

The moult of primaries, body feathers and non-streamer rectrices of Red-tailed Tropicbirds *Phaethon rubricauda* occurs outside the breeding season when individuals are at sea (Schreiber & Schreiber 1993). However, the two elongated central tail streamers are replaced continuously, with individuals almost always displaying one fully grown streamer while the other is still growing (Fleet 1974, Gould *et al.* 1974, Harrison 1990, Schreiber & Schreiber 1993). There is a lack of data in the literature regarding Tropicbird streamer moult; whether it is alternate, the rate at which the streamers grow and when moult occurs in

relation to breeding. For example, Schreiber and Ashmole (1970) stated that growth of one of the two streamers was often completed well before the other streamer emerged. Palmer (1962) suggested that streamers are moulted alternately. Streamers may require more time to grow to full length than does the rest of the plumage (Gould *et al.* 1974), but data are lacking. Approximately a dozen studies have used ptilochronology to measure feather growth rates in passerine birds (e.g. Grubb 1989, Grubb *et al.* 1991, Polo & Carrascal 1999, Jenkins *et al.* 2001, Stratford & Stouffer 2001, Carbonell *et al.* 2003), but no previous study has quantified feather growth in an adult seabird. Our objective was to quantify the patterns and timing of moult of tail streamers of the Red-tailed Tropicbird and aid understanding of the function of this unusual ornament.

METHODS

Study area and fieldwork

Fieldwork was carried out at a colony of more than 600 pairs of Red-tailed Tropicbirds at Tern Island, French Frigate Shoals Atoll in the north-western Hawaiian Islands (23°45'N, 166°15'W), from early April to mid August 2000, early February to mid May 2001, and January to February 2002. Tern Island, located near the north-western point of the atoll, is the largest (35 acres) of 10 sandy islets within French Frigate Shoals (Amerson 1971). At this location the Tropicbird breeding season is seasonally synchronous with most eggs laid between March and June. This contrasts with locations closer to the Equator such as Johnston Atoll (16°N, 169°W) and Christmas Island (2°N, 157°W) where some laying occurs in all months (Schreiber & Schreiber 1993).

Tropicbirds were captured by hand at nest-sites under shrubs (*Tournefortia argentea*) or buildings. Tropicbirds were ringed with a numbered stainless-steel leg ring; we recorded ring numbers of previously ringed birds. To provide blood for a genetic sexing technique, a 0.3-mL blood sample was collected from the tarsal vein of the left leg of most captured birds using a 22.5-gauge needle on a 1-mL syringe. The procedure took approximately 1 min. The blood sample was then transferred to a plastic vial containing 100% ethanol for preservation. We measured left and right streamer length (from insertion to tip on the ventral surface) to the nearest 1 mm using a 60-cm steel ruler. We took two independent measures to estimate measurement error. Independent measures were achieved by measuring the left streamer, then the right streamer, removing the ruler to re-position it at the left streamer for the second set of measurements. We recorded the status of nesting activity of each captured individual as not active or active (with egg or with chick).

Sex identification

For 236 individuals, sex was determined by genetic sexing of the blood samples (Fridolfsson & Ellegren 1999). For

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144 previously marked individuals, sex was determined by cloacal morphology (P. Sievert unpubl. data, 1998). P. Sievert checked nests daily, so the exact lay date was known. He examined the cloaca of one of the mates on the day of laying and the cloaca of the other mate when it returned from sea (1–10 days later). The pair member with the most distended cloaca (raised or thickened, usually by approximately 2 mm more) was judged to be the female. The diagnostic character was the thickening of the cloaca because the colour and diameter did not vary consistently. To confirm the cloacal sexing technique we tested blood samples of 47 birds (previously sexed by cloacal morphology) with the genetic technique and all were correctly sexed by P. Sievert.

Moult status of tail streamers

To determine whether the streamers were growing during the breeding season we examined each captured individual's central tail feathers carefully, checking the bases of the feathers for evidence of growth. Streamers were measured opportunistically when birds were present and captured at their nest-sites. A growing streamer was identified by the split white sheath remaining at its base. Measurements were taken of a growing streamer once the red feather was exposed from split white sheath (approximately 10 mm in length). Growing streamers were measured to lengths greater than 300 mm. New and old fully grown streamers were distinguished by colour (bright red vs. faded) and wear (unworn vs. abraded at the tip). Abrasion at the streamer tip was identified by missing vane (feathers) or the presence of worn whitish-pink vane at the tip. Recaptures and repeated measurements allowed us to confirm streamer growth or growth completion within individuals and to measure the time period between shedding of a streamer (e.g. when the streamer was dropped during handling) and a new feather sheath emerging. We also recorded cases of streamer breakage.

To quantify growth and wear, we measured left and right streamers of individuals recaptured within a year and between years (2000, 2001, 2002). To determine streamer growth rate (mm/day), we calculated the rate of change in streamer length for individuals measured two or more times within a breeding season. For individuals with multiple measurements, growth was based on the shortest interval (days) between two measurements. We also calculated the rate of wear (mm/day) at the tip of fully grown streamers measured two or more times within a breeding season.

Statistical analyses

Comparison of fully grown tail streamer lengths, growth rates and wear rates between males and females and between the breeding and non-breeding seasons were evaluated using unpaired *t*-tests. Chi-squared tests were used

to evaluate differences in proportions of males and females in tail streamer categories. We considered results as statistically significant at a value of $P < 0.05$.

RESULTS

Variation in tail streamer length and moult

Overall, we captured and measured 241 males, 192 females and 226 individuals of unknown sex. We found no evidence of moult of rectrices other than the central red streamers, nor did we observe any wing moult, in any individual we caught or observed. Of 1206 capture events, newly ringed individuals comprised 4% ($n = 50$), recaptures of birds ringed in years prior to our study 67% ($n = 807$) and recaptures within years comprised 29% ($n = 349$).

Fully grown tail streamers averaged significantly longer in males than in females [males, mean = 403 mm (se = ± 3.0), range = 277–524, $n = 221$, skewness = 0.78; females, mean = 388 mm (se = ± 3.2), range = 190–514, $n = 178$, skewness = 1.34; unpaired $t = 3.4$, $df = 397$, $P = 0.01$]. Measurement error, the percentage of total variability due to within-individual variation (Bailey & Byrnes 1990), was low: for 152 individuals with the left streamer measured twice, measurement error was < 1% with repeatability (r_1 , the intraclass correlation coefficient) essentially of 1.0.

Of 623 individuals measured at first capture during the three years of study, 68% had one fully grown tail streamer and the other streamer growing when measured (Table 1). We estimated that the delay between the loss of the older streamer and appearance of the emerging replacement feather sheath was about 1 week. One individual remeasured 9 days after the loss of its old streamer had a replacement streamer length of 11 mm, and another individual captured without any sign of one streamer was recaptured 7 days later without a feather sheath.

Seasonal patterns of streamer moult

At Tern Island, the Tropicbird breeding season commenced in January when adults arrived at the colony. Almost all breeding birds were brooding chicks by July (A.C.V. pers. obs., U.S.F.W.S. unpubl. data). In order to evaluate streamer moult in relation to the breeding season, we used the ratio of the lengths of the two streamers (Fig. 1). Ratios close to 1.0 represented two fully grown streamers or one fully grown streamer and one streamer nearly fully grown; ratios < 0.5 represented one fully grown streamer and one streamer beginning to grow. Early in the breeding season (before egg laying, January–March), many adults attending the breeding colony had one fully grown and one nearly fully grown streamer or two fully grown streamers (one old and one new, i.e. ratio = 0.7; Figs 2a & 3). After the majority of eggs were laid (early April), most birds either had one fully grown streamer

Table 1. Status of tail streamers of 623 Red-tailed Tropicbird individuals captured at Tern Island from January–July, 2000–2002.

Tail streamer categories	Male	Female	Unknown	All
2 fully grown	26	23	24	73 (12%)
1 fully grown, 1 growing	152	121	148	421 (68%)
1 fully grown, 1 absent ^a	39	32	34	105 (17%)
1 growing, 1 absent ^a	6	3	1	10 (2%)
1 broken, 1 absent ^a	1	1	1	3 (< 1%)
2 growing	2	3	5	10 (2%)
2 absent ^a	0	1	0	1 (< 1%)
Total	226	184	213	623

^aEither no trace of feather present or unsplit feather sheath present.

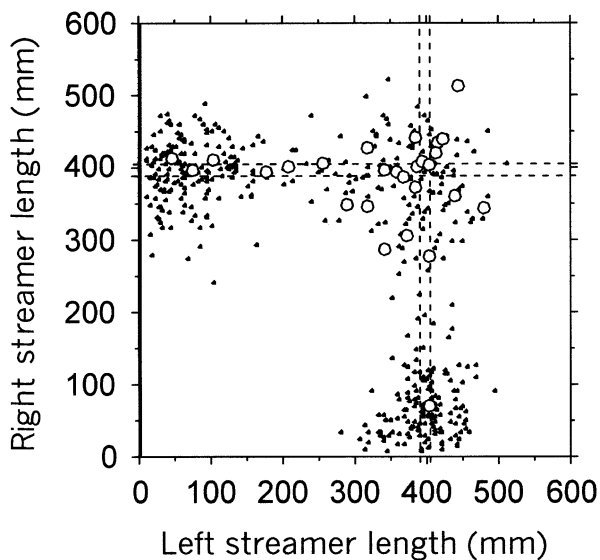


Figure 1. Right and left streamer lengths of 421 individual Red-tailed Tropicbirds at Tern Island, including 28 individuals (large open circles) measured within 1 week of laying (dashed lines indicate mean full-grown lengths for males and females, see text).

and the other just beginning to grow (i.e. ratio ≤ 0.4 , April–July) or one fully grown and one in pin (Fig. 3). Most breeding individuals retained two streamers up to about 1 week after the egg was laid; by 4 weeks after laying most individuals had dropped their worn streamer and begun to grow the replacement streamer (Fig. 3). For individuals with two fully grown streamers between January and April, the mean difference in length between the two streamers was 10.0 mm (paired $t_{82} = 1.6$, $P = 0.11$), with the older of the streamers being shorter in 51 of 83 (61%) cases. In 46 cases the longer of the two fully grown streamers was the left streamer and in 37 cases the longer was the right streamer (i.e. no evidence for bilateral asymmetry). The longest period over which individuals retained two fully grown streamers was 31 days. It appeared that

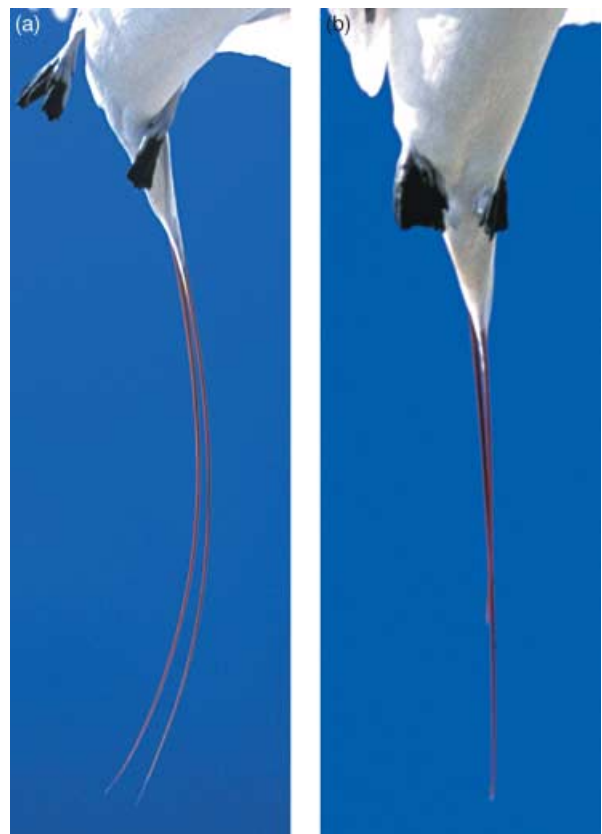


Figure 2. Red-tailed Tropicbird streamer expression at Tern Island. (a) A displaying individual with two fully grown streamers; (b) a non-displaying individual with one fully grown and one half-grown streamer.

previously mated individuals displayed two full-grown streamers and engaged in aerial courtship displays. A few birds were seen engaging in aerial displays with only one fully grown feather, but we were unable to compare the mating success of birds with one tail streamer with those that had two streamers.

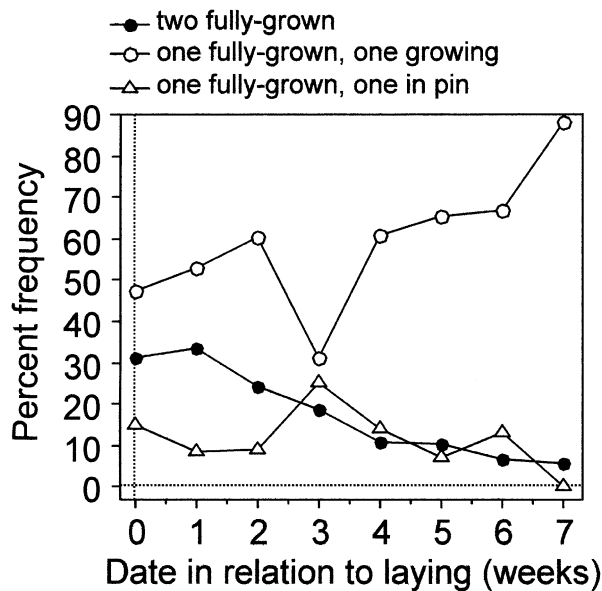


Figure 3. The timing of Red-tailed Tropicbird streamer moult relative to laying. Immediately after laying many birds had two fully grown streamers; later most birds had one fully grown streamer and one just beginning to grow.

Rates of streamer growth and wear

The mean growth rate of streamers was 2.2 mm/day (se = ± 0.04 , range = 0.5–3.9) with no difference between sexes (males = 2.2 mm/day and females = 2.3 mm/day, unpaired $t_{150} = 1.2$, $P = 0.2$). At this rate, a streamer of average length would take approximately 181 days (se = ± 6.4) to grow. For example, one individual's right streamer was absent for 87 days (14 April), was 84.5 mm on 21 May, 112.5 mm on 1 June, 132.5 mm on 8 June, 189.0 mm on 21 June and 209.0 mm on 10 July. We found no relationship between streamer growth rate and individual age in 31 individuals, aged 5–15 years, whose streamers were 50–150 mm in length ($r = 0.1$, $df = 30$, $P = 0.7$). There was no relationship between streamer growth rate and the interval (days) between measurements across 53 individuals measured twice within 15 days ($r = 0.2$, $df = 52$, $P = 0.2$). Only in 10 of 659 birds were both tail streamers growing simultaneously. In one case a female was captured with both streamers absent. Growth rate appeared to decline as streamers approached final length ($r = 0.4$, $df = 95$, $P < 0.001$, Fig. 4). The decline started only toward the end of the growth period. The mean wear rate of a fully grown streamer was 0.3 mm/day (se = ± 0.03 , range = 0.0–1.3) with no difference between sexes (males = 0.3 mm/day and females = 0.2 mm/day, unpaired $t_{101} = 0.7$, $P = 0.5$). Six per cent of individuals had one broken tail streamer when measured. We believe breakage was caused by wear and stress on streamers pressed against shrub branches.

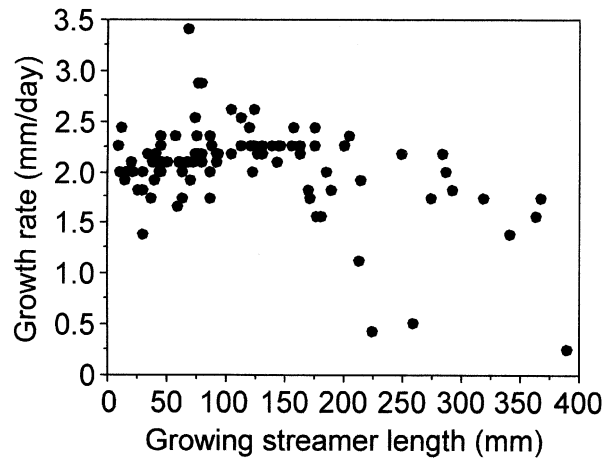


Figure 4. The relationship between length (at time of first measurement) and growth rate of moulting Red-tailed Tropicbird streamers.

From measurements of birds with two fully grown streamers during the January–April period, we can say that streamers grown during the season when most birds were incubating eggs and feeding chicks (February–July, about 6 months old, mean length = 392 mm) were only slightly shorter than streamers grown during the period when most birds were at sea (August–January, recently fully grown, mean length = 409 mm; unpaired $t_{118} = 2.1$, $P = 0.04$). Considering the effect of wear, these data suggest that streamers produced during the breeding and non-breeding seasons did not differ in length.

DISCUSSION

Tropicbird tail streamer moult appears to be unique and unlike any other reported pattern of tail feather moult in birds. Our measurements quantified for the first time the growth rate of these ornaments (a streamer required half a year to grow) and confirmed that the two streamers moult alternately. What can we infer regarding the function of these unusual feather structures from their moult patterns? First, the brief possession of two fully developed streamers during the period of maximal flight display and mate attraction prior to laying lends support to the idea that they serve primarily for optical displays during courtship. During Red-tailed Tropicbird display flights the paired streamers are conspicuously twitched from side to side by one bird in clear view of the other (Fleet 1974, Schreiber & Schreiber 1993). Indeed, the entire pattern of the flight display manoeuvres appears to be designed to show off the streamers, with courting birds trading places in positions from which the twitching red tails are viewed optimally. The possession of two fully grown streamers during the courtship period may signal a bird's readiness to breed; this may be important in a species in which breeding is not very synchronized at a population level, with different individuals initiating breeding over a 6-month

Erratum

Page 358, left column

Rates of streamer growth and wear

third sentence erroneously reads:

“For example, one individual’s right streamer was absent for 87 days [14 April], was 84.5 mm on 21 May, 112.5 mm on 1 June, 132.5 mm on 8 June, 189.0 mm on 21 June and 209.0 mm on 10 July.”

This sentence was changed by an editor; it should read (correct version):

“For example, over 87 days one individual’s right streamer was absent (14 April), 84.5 mm (21 May), 112.5 mm (1 June), 132.5 mm (8 June), 189.0 mm (21 June), and 209.0 mm (10 July).”

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span at Tern Island (Amerson 1971). At some other colonies, Red-tailed Tropicbird pairs may start breeding in any month of the year, possibly favouring the display of a conspicuous ornament that coordinates the pairing of individuals in similar states of readiness to breed. These points suggest that Red-tailed Tropicbird tail streamers are favoured by intersexual selection, probably involving mutual mate choice. However, because of the slow growth of streamers and the alternate pattern of moult, individuals do possess a partial streamer tail all year, even in the months when they are solitary at sea and not engaged in display. If moult during the non-breeding season is similar to that during the breeding season, individuals would also be expected briefly to possess two full-grown streamers during their period at sea. These points suggest that either the streamer tail has a function (unrelated to display) during the non-breeding period, or that for some reason the development of the paired streamer ornament requires a full year (6 months for each feather and sequentially) for growth. There is no obvious aerodynamic function for pin-tail ornaments such as Tropicbird tail streamers. Because the entire streamer projects beyond the point of maximum span of the tail, aerodynamic theory suggests that it cannot generate lift and thus will only cause drag (Thomas 1993). At present therefore it appears that Tropicbird tails are sexually selected ornaments with no function beyond that of courtship display (Balmford *et al.* 1993). If this is the case, then we require explanations for the lengthy growth period of the tail streamers and for the fact that they are produced one at a time rather than simultaneously as in most other avian feather ornaments. We require more information about Red-billed *Phaethon aethereus* and White-tailed Tropicbirds *Phaethon lepturus*, which have broader, more ribbon-like, more flexible and relatively longer streamers than do Red-tailed Tropicbirds. White-tailed Tropicbirds have been reported to moult just one of their two streamers each year (Lee & Walsh-McGehee 1998). Comparative study of moult patterns, causes of variation in fully grown streamer length and the use of the streamers in courtship displays of the three tropicbird species is required to understand the function of their extraordinary ornamental tails.

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