TAIL STREAMER FUNCTION AND SEXUAL SELECTION IN THE RED-TAILED TROPICBIRD

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TAIL STREAMER FUNCTION AND SEXUAL SELECTION IN THE RED-TAILED TROPICBIRD

by

Allison C. Veit

A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
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ABSTRACT –

The function of the elongated tail streamers of male and female Red-tailed Tropicbirds (*Phaethon rubricauda*) was studied on Tern Island (23°45' N, 166°15' W), French Frigate Shoals, Northwestern Hawaiian Islands from April to August 2000, February to May 2001, and January and February 2002. Adults were marked with a numbered steel leg band and sexed genetically or by cloacal morphology. Streamers are the two filamentous central rectrices, each with a black rachis and narrow red vane and averaging 399 mm in length when fully grown. The streamers molt alternately, with adults displaying one fully grown and one growing streamer throughout most of the year. The use of streamers in aerial courtship displays, together with the brief period when fully grown streamers coincide with the pre-laying period, strongly suggest a sexually-selected function for this spectacular tail ornament. My data are consistent with functions of tail streamers to attract mates, but suggest that variability in expression is arbitrary and hence streamers cannot signal an individual's "quality" in choice of mate.

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I dedicate this thesis to my parents Ed and Patricia Veit, my sister and her family Kristin, David, Benjamin, and Lauren Miller, and my sweet Phaethon whose love and support have been an inspiration. Thank you to my many great friends whose support and friendship helped me through this thesis and supplemented my time in the field with letters and care packages.

Tern Island, French Frigate Shoals holds a very special place in my heart and I feel privileged to have spent many years working and living at this magnificent site in the Northwestern Hawaiian Islands. Throughout this study I had the great pleasure to meet and work with many interesting and dedicated scientists. To all the friends I made in the field, each one of you added something special to my time on Tern Island and to those in Hawai'i, especially the Swimmer-Gorgas family, mahalo for your friendship and the occasional place to sleep when passing through the main islands.

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Chapter 1

General Introduction

1.1 Function of long tails

Bird tails vary greatly, from inconspicuous or vestigial as in some flightless birds such as the flightless cormorant (*Nannopterum harrisi)* to large, colorful ornaments as in the tail of male Indian Peafowl (*Pavo cristatus*). Bird tails have two main functions: in flight or as optical display structures. Aerodynamically, the tail produces lift (supplementing that created by the wings), influences flight maneuverability and agility, and assists in low flight speed (Thomas 1993, 1996, Norberg 1994, Thomas and Balmford 1995). The slender lifting surface theory (Jones 1990) predicts that only the part of the tail in front of the point of maximal continuous width is aerodynamically functional and the tail behind that point is relatively free from aerodynamic selection pressures (Thomas 1993). Extension of the tail beyond its point of maximal width increases drag but does not increase lift and is purely a costly addition (Evans and Thomas 1992, Balmford et al. 1993). The aerodynamically optimal tail is triangular in shape when spread and has a forked shape when folded, as the inner rectrices are shorter than the outer ones (Thomas 1993). In the pintails (*Anas acuta*), in which central rectrices are elongated as streamers, aerodynamic lift does not increase as the tail lengthens, and tail area and drag rise only slightly, therefore the marginal aerodynamic costs of tail elongation are relatively slight (Balmford et al. 1993). It is believed that Pintail streamers have arisen as sexually selected ornaments for display during the breeding season (Balmford et al. 1993, Thomas 1993).

Red-tailed Tropicbirds (*Phaethon rubricauda*) possess two elongated tail streamers, which are the two central tail rectrices. Such ornaments may signal individual "quality" via "good genes", or "handicap" process (Andersson 1986, Pomiankowski 1988) or may be arbitrary with the trait and preference for the trait coevolving in a spontaneous self-reinforcing "runaway" process (Fisher 1930, Kirkpatrick 1982, Lande 1980, Lande 1981). Ornaments that evolve through a signaling mechanism must be costly throughout their evolution; however ornaments that evolved through runaway selection need not have any cost (Thomas 1997). In some species sexual selection has influenced tail length or shape (Darwin 1871, Andersson 1994). Experimental evidence has shown that female Barn Swallows (*Hirundo rustica*), Jackson's Widowbirds (*Euplectes jacksoni*), Shaft-tailed Whydahs (*Vidua regia*), and Long-tailed Widowbirds (*Euplectes progne*) prefer males with the longest and most elaborate tails (Møller 1988, Andersson 1982, Andersson 1992, Barnard 1990). These studies examined female choice by experimentally lengthening and shortening tail ornaments. Males with longer tails had higher mating success and attained mates faster, mated earlier in the season and sometimes produced second clutches, mated with of higher-than-average quality females, and had more extra-pair copulations.

In this study, I set out to determine the function and explain the evolution of tail streamers of the Red-tailed Tropicbird by: 1) quantifying timing and patterns of growth in tail streamers; and 2) quantifying patterns of variation in tail streamers and other anatomical traits in relation to age and sex between two consecutive breeding seasons. This is the first study of the Red-tailed Tropicbird that provides quantitative information on tail streamers and only the second to investigate ornament variation in a socially monogamous sexually monomorphic bird species (Jones et al. 2000).

1.2 Structure of this thesis

This thesis is presented as a collection of two papers, written in preparation for publication in peer-reviewed international journals. Hence, a certain degree of overlap in introduction and methods is inevitable. Each paper will be co-authored by me and Ian L. Jones.

The present chapter outlines: 1) the function of long tails in birds; 2) natural history, taxonomy, and population status of the Red-tailed Tropicbird; and 3) the study site. Chapter 2 describes the tail streamer ornaments in relation to growth and patterns of molt. This paper has been submitted to Ibis. In Chapter 3, I quantify patterns of variation in tail streamer ornaments and other traits in relation to age and sex. This paper has been submitted to The Auk. A summary is presented in Chapter 4.

1.3 Natural history, taxonomy, and population status

Red-tailed Tropicbirds are socially monogamous, monochromatic tropical seabirds of medium size. Adults have almost all-white plumage, black feet, a bright red or orange bill, and two long central red rectrices (streamers). Prior to breeding, adult Red-tailed Tropicbirds display their red central tail streamers conspicuously to individuals of the opposite sex during aerial courtship displays in which pairs fly backward loops around each other while slowly twitching the streamers from side to side and vocalizing loudly (Fleet 1974, Schreiber and Schreiber 1993, ACV and ILJ, pers obs). A pair will land on the ground at a prospective nest site, where they remain sitting side by side until resuming aerial displays with one another (ACV pers obs). Nests are usually simple scrapes on the ground under shrubs or structures in which a female lays a single red-speckled egg. Throughout the breeding season, both adults equally share parental care. Individuals with a nest that is occupied with an egg or a chick do not perform aerial displays and spend their time at sea except when attending the nest (Fleet 1974, Schreiber & Schreiber 1993, ACV pers obs).

Red-tailed Tropicbirds are common breeding seabirds on tropical and subtropical oceanic islands in the Pacific and Indian Oceans. Four subspecies have been described: *rubricauda* - western Indian Ocean; *westralis* - Indian Ocean on Cocos-Keeling, Christmas Island, off western Australia; *roseotincta* - Raine, Herald, Coringa, Lord Howe, Norfolk, and Kermadec islands in the southwestern Pacific Ocean; *melanorhynchos* - rest of Pacific Ocean (American Ornithologists' Union 1983). Tarbuton (1989) suggested that subspecific recognition was unwarranted, based on culmen and wing measurements. The conventionally recognized subspecies appear to form a north-south cline in plumage tone and measurements (Del Hoyo et al. 1992). Populations in the Pacific Ocean were estimated at 31,000 birds in the late 1960s (Gould et al. 1974) and were considered stable. Most nesting islands are in remote areas of the Pacific and are rarely visited by scientists, so population trends are poorly known (Schreiber and Schreiber 1993). Tropicbirds are not globally threatened, but have suffered extensive human exploitation for food and from introduced predators, especially feral cats (*Felis catus*) and rats (*Rattus exulans*). In much of the Pacific range the bright red tail streamers are also taken by humans for ornamental purposes.

1.4 Study site

Large numbers of tropicbirds breed in the Northwestern Hawaiian Islands, which consist of ten islands and atolls that stretch 1770 km across the middle of the North Pacific Ocean. French Frigate Shoals (23°45' N, 166°15' W) is the midpoint of the Hawaiian Archipelago and lie approximately 800 km northwest of Oahu. "Shoal of the French Frigates" was discovered in November 1786 by Count La Pérouse, who narrowly averted running aground on the surrounding barrier coral reef. The first scientific visit was recorded in 1859 (Amerson 1971). French Frigate Shoals is part of the Hawaiian Islands National Wildlife Refuge (HINWR) under the protection and management of the U.S. Fish and Wildlife Service. In response to heavy pressure from sealers, feather hunters, fishermen, and guano miners - who killed many of the seals, seabirds, and sea turtles during the 19th century - President Theodore Roosevelt created the Hawaiian Islands Bird Reservation (now known as HINWR) to protect the wildlife in 1909 (Rauzon 2001). French Frigate Shoals again came under pressure when it became a strategically important location for the U.S. military in World War II (Amerson 1971). In 1942, as a direct result of the Battle of Midway and in response to the war in the Pacific, the U.S Navy constructed Tern Island. The original six-acre Little Tern Island was enlarged to 35 acres by erecting a seawall filled with dredged crushed coral. The island resembled an aircraft carrier and provided fueling and landing facilities for aircraft that ferried between Pearl Harbor and Midway. After World War II, Tern Island was initially utilized by Hawaiian commercial fishermen and in 1952 the U.S. Coastguard constructed a LORAN transmitting station on the island (Amerson 1971). In 1979, Tern Island became a permanent biological field station maintained by the U.S. Fish and Wildlife Service.

Tern Island is home to sixteen species of breeding seabirds, including 80,000 pairs of Sooty Terns (*Sterna fuscata*) making it the third largest tern colony in Hawai'i (Rauzon 2001). The island offers opportunities for researchers to conduct studies on large numbers of seabirds with many marked individuals. Tern Island has approximately 600 breeding pairs of Red-tailed Tropicbirds (many banded as chicks) that occupy nest sites under shrubs or buildings. Two of the 12 islands in the atoll (Tern and East) provide suitable nesting habitat for the Red-tailed Tropicbird.

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Chapter 2

Timing and patterns of growth in tail streamer ornaments of the Red-tailed Tropicbird

2.1 Abstract

I investigated timing and patterns of molt of tail streamers (central two rectrices) in the Red-tailed Tropicbird (*Phaethon rubricauda*) based on 659 individuals (including 401 of known age and 432 of known sex), measured in 2000-2002 at Tern Island, French Frigate Shoals, Hawai'i. Tail streamers are hypothesized to be the product of sexual selection because they may have no clear aerodynamic function but serve as ornaments displayed during the breeding season for the purposes of mate attraction (Balmford et al. 1993a). The streamers are filamentous with a black rachis and narrow red vane and average 399 ± 1.8 SE mm in length when fully grown ($n = 607$, range 190 - 524). At the beginning of the breeding season (pre-laying and laying) most individuals had two fully grown streamers (one freshly grown, one about six months old) or one fully grown and one nearly fully grown. During incubation and chick-rearing, 64% had one fully grown streamer and the other growing. Streamer growth rate averaged 2.2 ± 0.1 mm day^{-1}, slowing as the feather approached full length and taking 181 ± 6.4 days to reach full length; each fully grown streamer was retained for six months. The two streamers molted alternately, with adults displaying at least one fully grown streamer throughout the year (excepting cases of breakage). Streamers molted during summer and winter did not differ in length. Streamer length differed slightly between male (403 mm) and female (388 mm) but molt patterns did not differ between sexes. The display of two fully grown streamers during courtship is likely under sexual selection and may signal readiness to breed.

2.2 Introduction

Tail streamers, facial crests, and facial plumes are widespread in birds as optical display structures. They vary in expression between sexes, with age, and among individuals (Andersson 1994). Tail streamers (elongated central rectrices) are hypothesized to be the product of sexual selection because they may have no clear aerodynamic function but serve as ornaments displayed during the breeding season for the purposes of mate attraction and intra-sexual competition (Balmford et al. 1993a). To understand the function of plumage ornamentation, it is necessary to understand molt, including loss of old feathers and growth of new (Ginn and Melville 1983). General pattern of molt and growth of rectrices is generally described as continual stepwise molt (Stresemann and Stresemann 1966). Rectrices typically molt centrifugally from the innermost pair to the outermost pair and occur after breeding. In contrast, the two elongated central rectrices of the Red-tailed Tropicbird grow alternately and slowly, with one usually growing throughout the year.

Tropicbirds (Pelecaniformes; Phaethontidae) include three socially monogamous, tropical seabird species, all of which have conspicuous tail streamers. Adults have 14 rectrices, including the narrow and flexible streamers that are important in the optical signaling in courtship (Del Hoyo et al. 1992, Gould et al. 1974). Molt of streamers has not been quantified in detail (Schreiber and Schreiber 1993). Unlike most birds (Stresemann and Stresemann 1966), the central rectrices of tropicbirds are replaced continuously, with one streamer almost always fully grown and the other growing (Fleet 1974, Gould et al. 1974, Harrison 1990, Schreiber and Schreiber 1993). However, there is confusion in the literature about molt: whether it is alternate, the rate at which streamers grow, and when molt occurs in relation to breeding. For example, Schreiber and Ashmole (1970) found that growth of one streamer was often completed well before the other streamer emerged, contradicting (Palmer 1962) who suggested that streamers are molted 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. Several studies have measured feather growth rates in avian populations using ptilochronology (Grubb 1989, Grubb et al. 1991, Dolby and Grubb 1998, Grubb 1998, Stratford and Stouffer 2001). However, no study has investigated molt of tail streamers in a socially monogamous, sexually monomorphic species. My objective was to quantify patterns and timing of molt of tail streamers of the Red-tailed Tropicbird, to resolve confusion in the literature, and aid understanding of the function of this unusual ornament.

2.3 Methods

Field work was carried out at a colony of more than 600 pairs of Red-tailed Tropicbirds at Tern Island, French Frigate Shoals in the Northwestern Hawaiian Islands (23°45' N, 166°15' W), from early April to mid August 2000, early February to mid May 2001, and January and February 2002. Tern Island, located near the northwestern point of the atoll, is the largest (35 acres) of ten sandy islets within the atoll (Amerson 1971). At this location the tropicbird breeding season is more seasonally synchronous (majority of egg laying occurs from March to June) than 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 and Schreiber 1993).

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; I recorded band numbers of previously banded birds. To determine sex a 0.3 ml blood sample was collected from the tarsal vein of the left leg using a 22.5 gauge sterile needle. The needle punctured the vein and blood was slowly drawn into a 1ml syringe. The procedure took approximately a minute. The blood sample was then transferred to a plastic vial containing a small amount of 100% ethanol for preservation and storage. I 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. I took two measures to estimate measurement error. 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. I recorded the status of nesting activity as not active or active (with egg) or active (with chick). For most individuals, sex was determined by genetic sexing (Fridolfsson and Ellegren 1999). Some previously marked individuals had been sexed based on cloacal morphology (P. Sievert, unpublished data, 1998). Sievert checked nests daily, so the exact lay date was known. He examined the cloacal 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). In females the perimeter of the cloacal was raised or thickened, approximately 2 mm more than in the males. The diameters of the male and female cloacals were fairly consistently at 10 mm. To confirm sexing by cloacal morphology, some individuals sexed by Seivert were checked by genetic sexing.

In addition to measuring each streamer to the nearest mm, I determined the molt status of streamers during the breeding season. I examined each feather carefully, checking the bases of the feathers for evidence of growth and assigned each feather a score (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 was a pinfeather within a sheath with no exposed feather. A score of 2, 3, and 4 indicated growing. A growing streamer had a whitish sheath remaining at the base and was ranked by length: 2 (10 to 199 mm), 3 (200 to 299 mm), and 4 (300 mm to fully grown). A growing streamer was first measured at approximately 10 mm in length (feather exposed from sheath) and still growing at a length greater than 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 versus faded) and wear (unworn versus abraded at the tip). The states of color were not coded. Abrasion at the tip was defined as missing vane (feathers) or a whitish-pink vane at the tip. A few individuals that were not scored in 2000 (i.e., base of streamer not examined) were assigned a score later, if repeated measurements were taken within the year. Streamers were measured opportunistically when birds were present at the nest site. In some cases, repeated measurements allowed for confirmation of whether a streamer was growing or fully grown and to determine the period between shedding a streamer (when the streamer molted in hand) and a new pin emerging. To quantify growth and wear, I measured left and right streamers of individuals recaptured within a year and between years (2000, 2001, and 2002). I also noted breakage at the feather tip.

To determine growth rate (mm day^{-1}) of streamers, I calculated 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 fewest interval (days) between two measurements. I also calculated rate of wear (mm day^{-1}) at the apical end of fully grown streamers measured two or more times within a breeding season.

To examine the relationship between molt and breeding, I identified male and female pair members and monitored nests ($n = 60$) throughout two breeding seasons.

All statistical tests were performed using StatView 5.0. Comparison of fully grown streamer lengths, growth rates, and wear rates between males and females and between 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 streamer categories. All reported values are means ± SE. I considered results as statistically significant if $P < 0.05$.

2.4 Results

Overall, I captured and measured 241 males, 192 females, and 226 individuals of unknown sex. I retrapped 349 birds within and 807 between years (2000, 2001, and 2002) for a total of 1206 captures.

Fully grown streamers averaged significantly longer in males than in females (males, mean = 403 ± 3.0 mm, range = 277 – 524, $n = 221$, skewness = 0.78; females, mean = 388 ± 3.2 mm, range = 190 - 514, n = 178, skewness = 1.34; unpaired t = 3.4, df = 397, P = 0.01, Figure 2.1). Measurement error, the percent of total variability due to within-individual variation (Bailey and Byrnes 1990), was low: for 152 individuals with the left streamer measured twice, measurement error was < 1% with repeatability (r_I, the intra-class correlation coefficient) of 1.0.

On Tern Island, the tropicbird breeding season commenced in January when adults arrived at the colony. The majority of egg laying occurred from late March to early April and almost all breeding birds were brooding chicks by July (data available from ACV, U.S. Fish and Wildlife Service unpublished data). Based on 659 individuals captured and measured during the three years of study, 64% had one fully grown tail streamer and the other streamer growing when measured (Table 2.1, Figure 2.2). There was no difference between males and females in the proportion of individuals in the three most frequently occurring tail streamer categories; two fully grown, 1 fully grown and 1 growing, and 1 fully grown and 1 absent ($\chi^2 = 2.0$, df = 2, $P = 0.4$). I found very few birds with no trace of one of the streamers and estimate the period between the loss of a streamer and appearance of the pinfeather as about a week, but variable. The period between shedding a streamer and a pin emerging was estimated when a streamer molted in hand. In one case, the individual was remeasured nine days later with a streamer length of 10.5 mm. In another case, an individual was measured without a streamer (0 mm), and then remeasured seven days later again without a pin feather (0 mm).

In order to evaluate streamer molt in relation to the breeding season, I calculated the mean ratio of both streamers. 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, Jan-Mar), most 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). After the majority of eggs were laid (early April), most birds had one fully grown streamer and one beginning to grow (i.e. ratio ≤ 0.4, Apr-Jul) or one fully grown and one in pin. The older of the two streamers had dropped (molted) and a new streamer was beginning to grow in its place (Figure 2.3).

Most breeding individuals retained two streamers up to about a week after the egg was laid; by four weeks after laying most individuals had dropped their worn streamer and begun to grow the replacement streamer (Figure 2.4). For individuals with two fully grown streamers during January through 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 47 cases the longer of the two fully grown streamers was the left streamer and in 37 cases the longer was the right one (no evidence for bilateral asymmetry). The longest period over which individuals retained two fully grown streamers was 31 days.

Table 2.1 Red-tailed Tropicbird tail streamer status of 659 individuals captured at Tern Island from January–July, 2000-2002.

Tail streamer categories	**male**	**female**	**unknown**	**all**
2 fully grown	26	23	24	73 (11%)
1 fully grown, 1 growing	152	121	148	421 (64%)
1 fully grown, 1 absent[1]	39	32	34	105 (16%)
1 fully grown, 1 broken	3	1	2	6 (<1%)
1 growing, 1 broken	11	6	11	28 (4%)
1 growing, 1 absent[1]	6	3	1	10 (2%)
2 broken	1	1	0	2 (<1%)
1 broken, 1 absent[1]	1	1	1	3 (<1%)
2 growing	2	3	5	10 (2%)
2 absent[1]	0	1	0	1 (<1%)
totals:	241	192	226	659

[1] either no trace of feather present or pin present

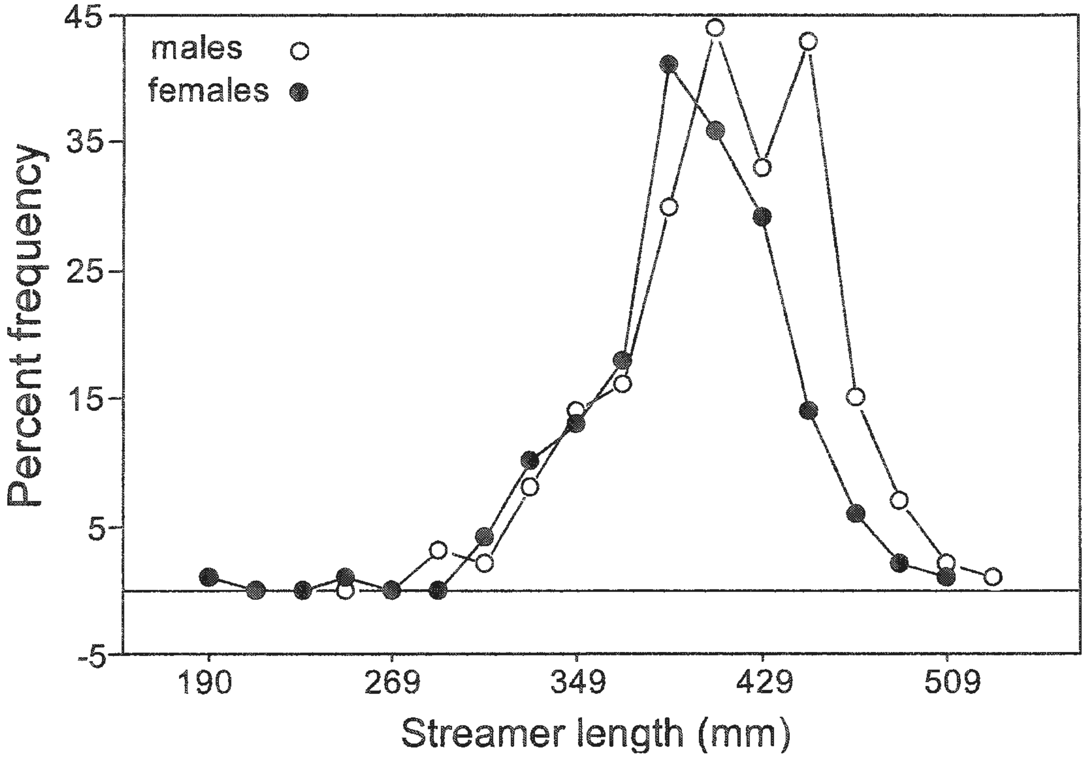

Figure 2.1 Frequency distribution for fully grown tail streamer length in Red-tailed Tropicbirds (*n* = 218 males and *n* = 176 females measured).

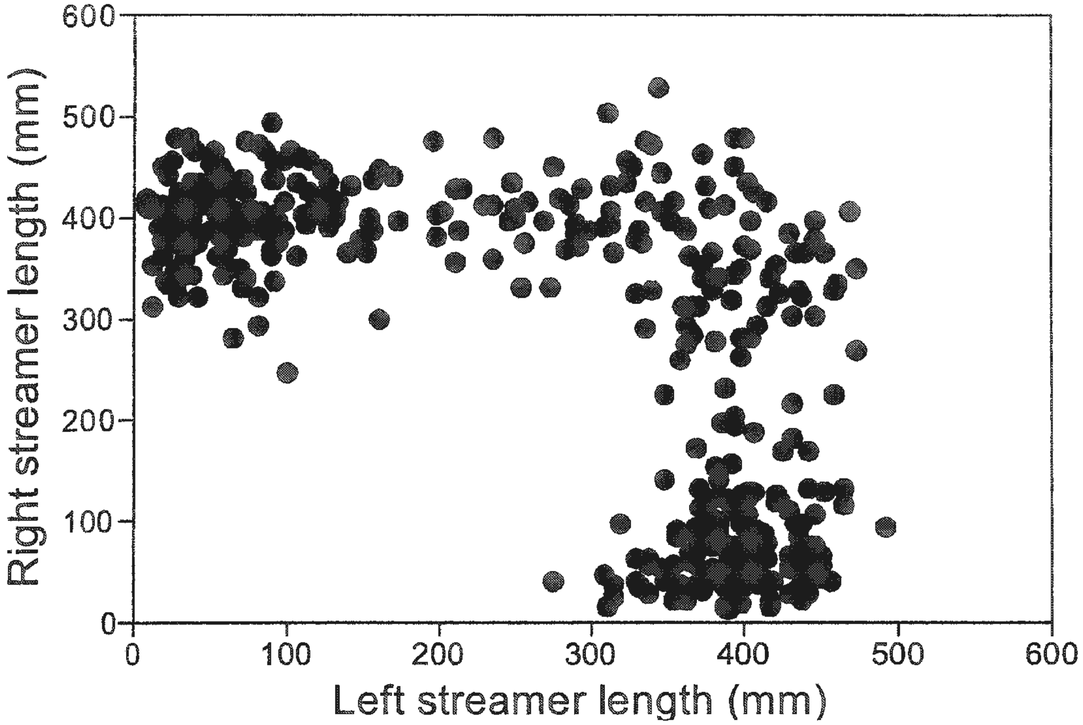

Figure 2.2 Plot of the right and left streamer lengths based on 421 Red-tailed Tropicbirds with one streamer fully grown and the other growing.

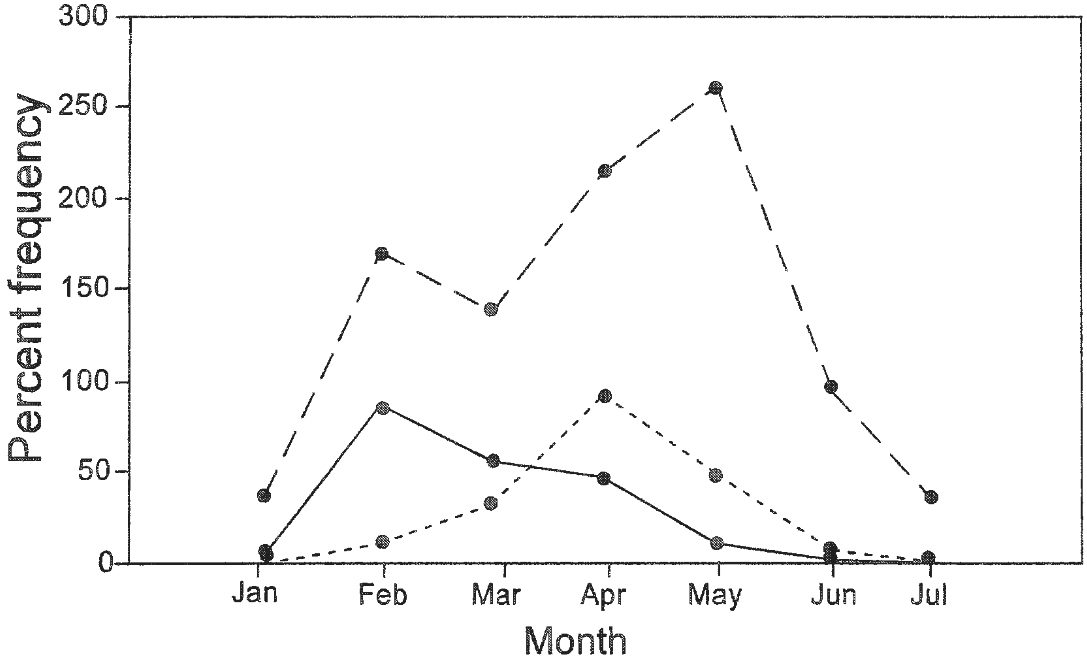

Figure 2.3 The seasonal pattern of Red-tailed Tropicbird streamer molt at Tern Island. Early in the breeding season most individuals have one fully grown and one (long) growing streamer (– – –) or two fully grown streamers (——). After the majority of eggs are laid, most birds had one fully grown streamer and one in pin (- - -).

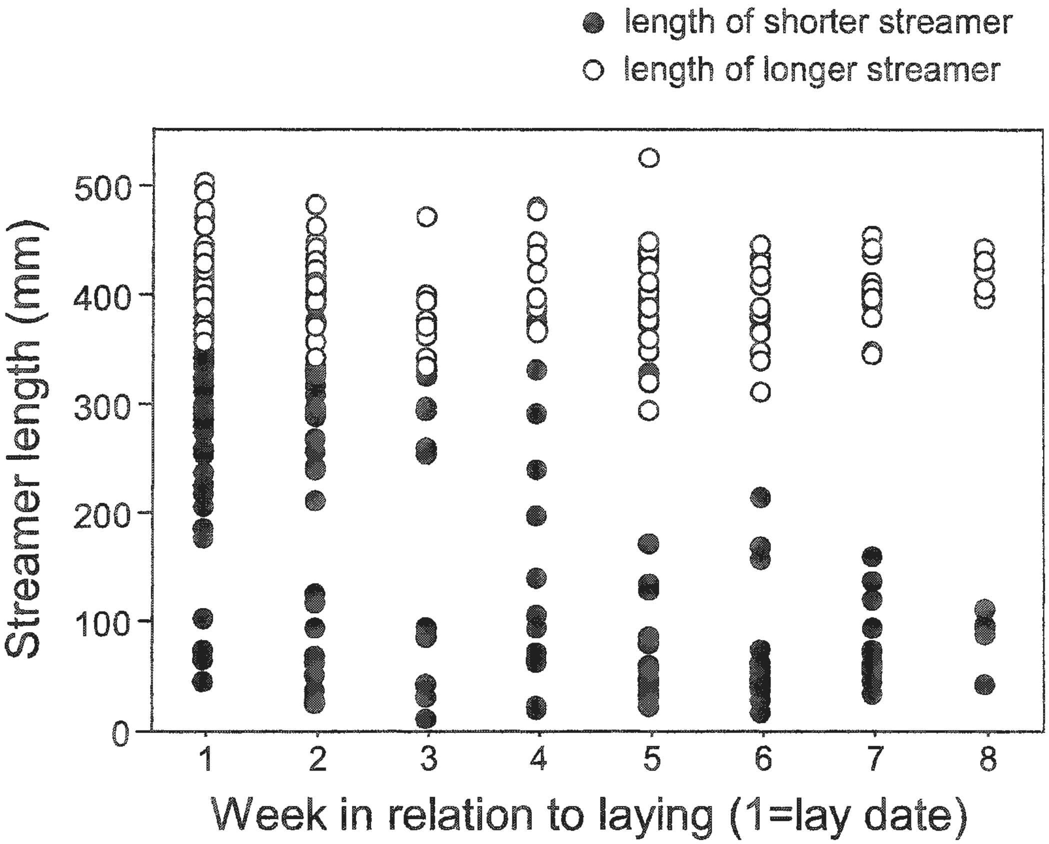

Figure 2.4 The timing of Red-tailed Tropicbird streamer molt relative to laying, as indicated by length of the longer streamer and the length of the shorter streamer. Immediately after laying most birds had two fully grown streamers, later most birds had one fully grown streamer and one beginning to grow.

Mean growth rate of streamers was 2.2 ± 0.04 mm day^{-1} (range = 0.5 – 3.9) with no difference between sexes (males = 2.2 mm day^{-1}and females = 2.3 mm day^{-1}, unpaired $t_{150} = 1.2$, $P = 0.2$). At this rate, a streamer of average length would take approximately 181 ± 6.4 days to grow. For example, over 87 days one individual's right streamer was 0.0 mm (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). There was no relationship between streamer growth rate and age of an individual, based on 31 individuals 5-15 years old whose streamers were 50 to 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, based on 53 individuals measured twice within 15 days ($r = 0.2$, df = 52, $P = 0.2$; Figure 2.5). Only in 10 of 659 birds were both tail streamers growing simultaneously. Because streamers grow alternately, the growing streamer requires energy and nutrient while the one that is fully grown or nearly fully grown requires none. In one case a female was captured with both streamers absent. Growth rate declined as streamers approached final length ($r = 0.4$, df = 95, $P < 0.001$; Figure 2.6). The decline started only toward the end of the growth period. The mean wear rate of a streamer was 0.3 ± 0.03 mm day^{-1} (range = 0.0 – 1.3) with no difference between sexes (males = 0.3 mm day^{-1} and females = 0.2 mm day^{-1}, unpaired t_{101}= 0.7, $P = 0.5$). Six percent of individuals had one broken tail streamer when measured. Breakage was caused by wear and the stress of a streamer pressed against shrub branches at the nest site.

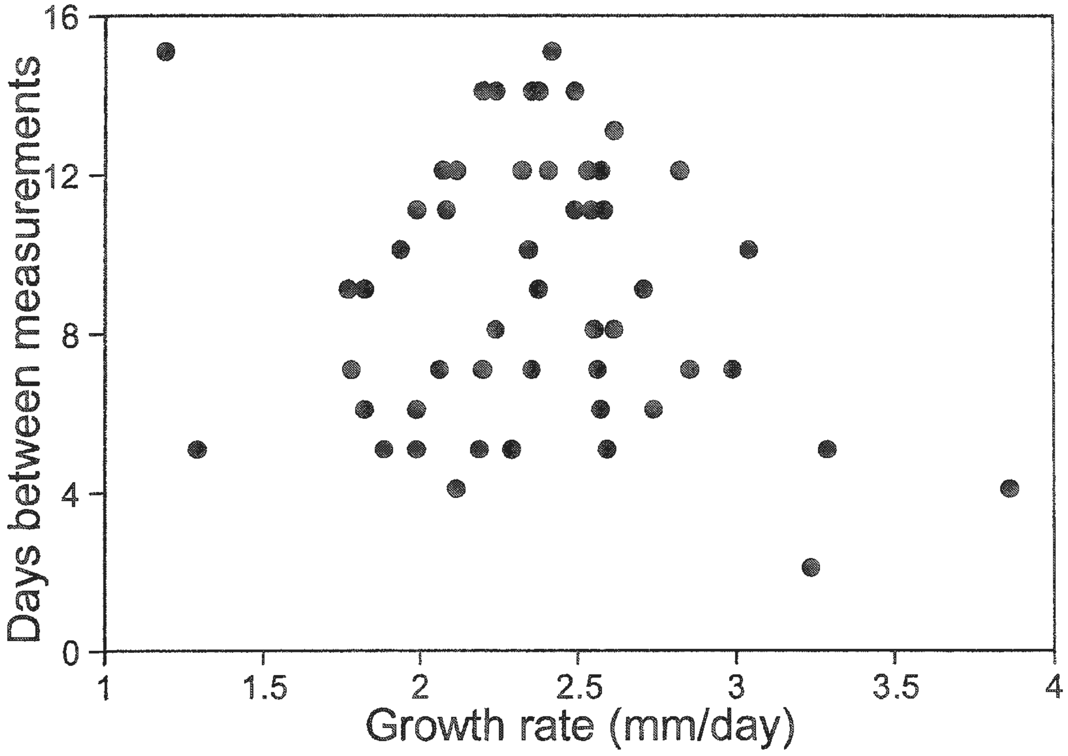

Figure 2.5 Plot of interval (days) between measurements versus growth rate. There was no significant relationship.

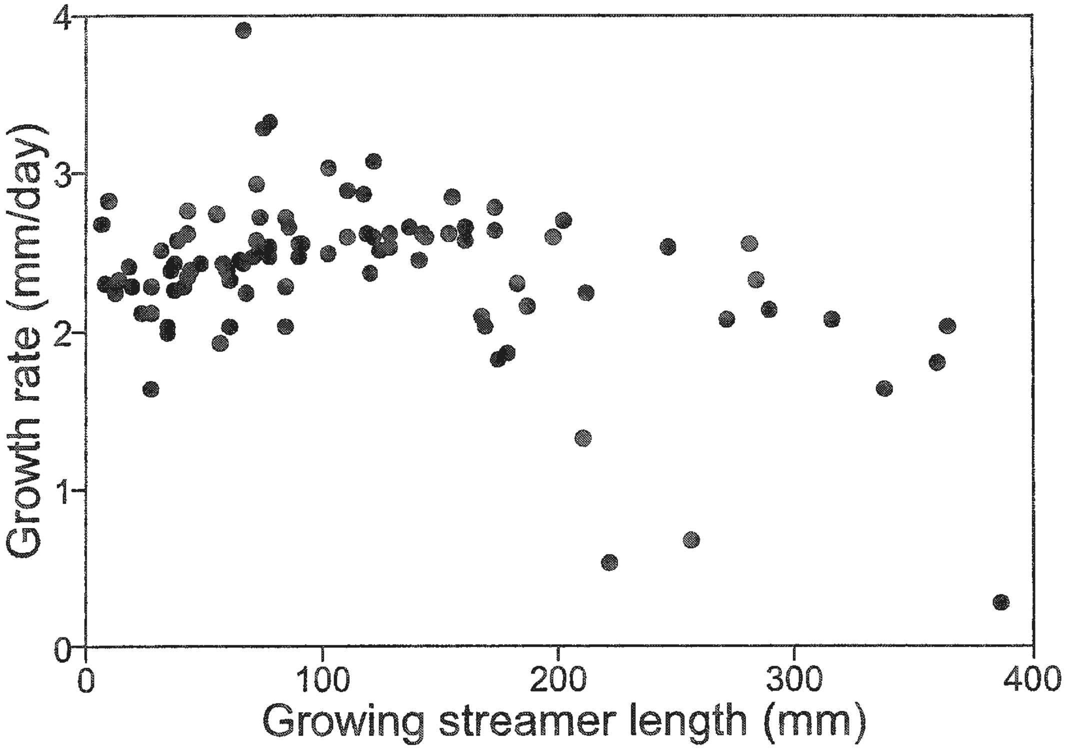

Figure 2.6 The relationship between growth rate and length of molting Red-tailed Tropicbird streamers. Rate of growth declined as streamer reached full length.

Based on measurements of birds with two fully grown streamers during the January-April period, streamers grown during the season when most birds were incubating eggs and feeding chicks (February-July, about six months old, mean length = 392 mm) were only slightly shorter than streamers grown when most birds were at sea (August to January, recently fully grown, mean length = 409 mm; unpaired $t_{118} = 2.1$, $P = 0.04$; Figure 2.7). Considering the effect of wear, these data suggest that streamers produced during the breeding and non-breeding seasons did not differ in length.

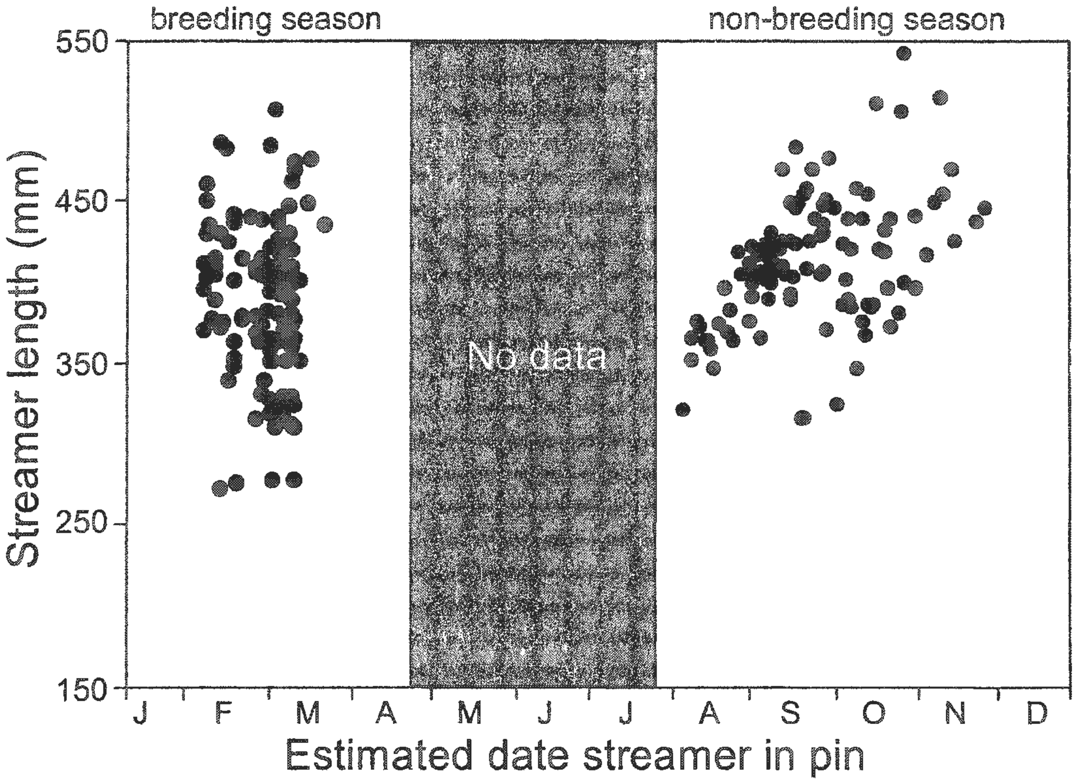

Fig. 2.7 Fully-grown streamers grown during the breeding and non-breeding season graphed according to the estimated date each feather was in pin (i.e., timing of the beginning of growth). Streamers produced during the breeding and non-breeding seasons did not differ in length.

2.5 Discussion

Tropicbird tail streamer molt is unique and unlike any reported pattern of tail feather molt, with extremely slow growth (a streamer takes half of a year to grow) and alternate molt of the two streamers. The slow growth rate may function to spread the cost of molt over the entire year and thus reduce stress. Although birds display at least one streamer year round, the coincidence of two fully developed streamers during the period of maximal flight display and mate attraction lends support to the idea that they serve primarily for optical communication during courtship.

Taken together, my data indicate the two tail streamers grow alternately, with individuals having one fully grown streamer and one molting streamer during most of the year, and usually two fully grown streamers in the weeks before laying, perhaps signaling readiness to breed during the period of intense courtship display. The year-round possession of at least one streamer may imply an aerodynamic role; further work is required to investigate streamer function.

2.6 Acknowledgments

I thank the Hawaiian Islands National Wildlife Refuge, U.S. Fish and Wildlife Service of the Department of the Interior, in particular David Johnson, Elizabeth Flint, Dominique Horvath and the Tern Island staff for logistic support and permission to conduct research at Tern Island, French Frigate Shoals, Steve Carr and Dawn Marshall for assistance with genetic sexing of blood samples. My study was supported by funding from Memorial University of Newfoundland and the Natural Sciences and Engineering Research Council of Canada.

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Chapter 3

The function of tail streamers of Red-tailed Tropicbirds (*Phaethon rubricauda*) as inferred from patterns of variation

3.1 Abstract

I investigated the functions of Red-tailed Tropicbird (*Phaethon rubricauda*) tail streamers by quantifying patterns of variation in streamers and other measurable traits based on 659 individuals, including 422 of known age and 459 of known sex, measured in the field from 2000 to 2002. Prior to breeding individuals of opposite sex conspicuously display elongated red tail streamers during complex aerial courtship. As in other putative sexually selected traits, tail streamers were more variable than non-ornamental traits across individuals with males slightly larger than females in length of fully grown streamers (ratio 1.04), culmen length (ratio 1.02), and tarsal length (ratio 1.01). Ratio represents sexual dimorphism index (male trait size/female trait size). There was no correlation between length of fully grown streamer and body size (score on first principal component) ($r = 0.06$) or wing length (males, $r = 0.01$, females $r = 0.1$) 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 = 0.5) of male and female pair members indicating that ornament expression is synchronized within pairs. However, tail streamers do not appear to be good indicators of individual's "quality": based on 372 adults of known age (3–22 years), streamer length did not increase with age ($r = 0.3$) 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 correlated with egg size. My data are consistent with the idea that Red-tailed Tropicbird's tail streamer ornaments function for mate attraction, but suggest that

variability in their expression is arbitrary and unlikely to provide a meaningful signal of individual quality during mate choice.

3.2 Introduction

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). For example in the Long-tailed Widowbird, *Euplectes progne,* experimental evidence has demonstrated that the tail of the male is favored by female choice. By lengthening male's tails by 20-30 cm Andersson (1982) found elongated males were more successful (higher mean number of nests per male) than males with shortened or control tails. Females preferred males with supernormal tails, as the elongated males had highest success (Andersson 1994). Such sexually selected ornamental traits exhibit high levels of variation compared with traits thought to be due to other forms of natural selection (Alatalo et al. 1988, Jones and Montgomerie 1992, Evans and Barnard 1995, Jones et al. 2000). This variation has been suggested to result from lack of stabilizing selection on these ornamental traits (Alatalo et al. 1988) and the tendency for ornaments to be costly and sometimes correlated with individual health (e.g., Møller 1991). Tail streamer ornaments formed by elongated central rectrices (pin tails) no known beneficial aerodynamic function but instead have arisen as sexually selected ornaments that function to attract mates or in intra-sexual competition (Balmford et al. 1993, Thomas 1993). In some polygynous birds there is male-biased sexual dimorphism and high variability of the male ornaments (e.g., Petrie et al. 1991), while in some monogamous species the males and females (sexes monomorphic) may have similar ornaments that are favored by mutual sexual selection (Jones and Hunter 1993, Jones and Hunter 1999). While sexual selection is widely accepted as the foremost evolutionary explanation of male ornaments, little attention has been given to ornaments occurring in females. Female ornamentation has been considered as nonadaptive effects of selection on males. However, recent studies provide evidence that female ornamentation is not severely constrained by selection on males and has evolved independently of male showiness. Thus selection acting on females may be a cause of female ornaments (Amundsen 2000). There are few studies (e.g., Jones et al. 2000) that have investigated ornament variation in a monogamous sexually monomorphic bird species.

The adult Red-tailed Tropicbird is pigeon-sized (650-780 g) with satiny white plumage, a strong pointed red-orange bill, and two flexible elongated red central feathers that form conspicuous tail streamers about 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 or actively flies backward, 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), with the same behaviour observed on Tern Island. This scene presents a biologist with an improbable sight. What is the function of the red streamers, and what mechanism could possibly explain their evolution? The use of the streamers in these displays, together with the finding that adults' brief possession of two fully grown streamers coincides with their pre-laying period (Chapter 2), strongly suggests a sexually selected function for tail streamers. 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, suggesting that they are unlikely to enhance flight performance (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, I looked for an allometric relationship between tail length and both wing length and body size (PC1). I predicted that if Red-tailed Tropicbird tail streamers have a significant flight function, they should correlate with other aerodynamically important traits such as wing length across individuals.

In this study I 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 vigour I attempted to estimate (1) effects of age and year on ornamental expression, and (2) relations of ornamental size to body condition and breeding performance. Finally, I investigated assortative mating related to ornaments. Due to the active nature of tropicbird flight displays and the logistical difficulties encountered when attempting to follow marked individuals, intensive behavioral observations were not collected.

I evaluated my 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 intra-sexual selection. Within hypothesis two I considered two alternatives: 1) streamers are condition-dependent indicators of individual quality (i.e., a 'good genes', or 'handicap' process, Andersson 1986, Pomiankowski 1988); and 2) 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, Lande 1981, or sensory exploitation, Ryan and Rand 1993).

3.3 Methods

Field work was carried out at a colony of more than 600 pairs of Red-tailed Tropicbirds at Tern Island, French Frigate Shoals in the Northwestern Hawaiian Islands (23°45' N, 166°15' W), from early April to mid August 2000, early February to mid May 2001, and January and 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; I recorded band numbers of previously banded birds. To determine sex a 0.3 ml blood sample was collected from the tarsal vein of the left leg using a 22.5 gauge sterile needle. The needle punctured the vein and blood was slowly drawn into a 1ml syringe. The procedure took approximately a minute. 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 scaled comparison of variation in body mass with variation in linear variables. Linear measurements taken were: 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 nostrils), diagonal length of tarsus (on left leg, from midpoint of tibiotarsal joint to distal end of tarsometatarsal joint on underside of 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), total head length (from tip of bill to occipital condyle) were measured to the nearest 1 mm using a 45cm stainless steel wing ruler and left and right streamer length (from insertion to tip, on ventral surface) to nearest 1 mm using a 60cm stainless steel ruler. All measurements were taken by the same person (ACV). I inspected the bases of both streamers for evidence of molt and assigned a score (for protocol see Chapter 2). Two independent measures of wing and streamer lengths were taken to quantify measurement error and repeatability. Measurement error (ME), the proportion of within-individual variation to total variation was calculated as $ME = MS_{within}/(s^2_{among}+MS_{within})$ x 100%. Ostle and Mensing (1975) estimated $s^2_{among} = MS_{among}-MS_{within}/3$ measurements per individual. Repeatability of measurements within measurer was defined as r_I, the intra-class correlation coefficient (Bailey and Byrnes 1990). 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. I recorded the status of nesting activity as not active or active (with egg) or active (with chick). 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 (Sievert unpubl. data). To determine sex by cloacal morphology see Chapter 2 for protocol.

To determine the best measure of streamer size it was necessary to consider the molt sequence. In many species, ornamental rectrices develop simultaneously and completely prior to the breeding season; this is not the case in the Red-tailed Tropicbird. Tropicbird streamers molt alternately, with each streamer taking about six months to complete growth; the streamer is retained at full length for approximately six months thereafter (Chapter 2). 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 (Chapter 2). I used the length of one fully grown streamer (right or left side) to quantify ornament size. Individuals included in the analysis were those with a fully grown streamer that showed no signs of wear at the tip or breakage along its length.

To quantify temporal variation in ornament expression, I compared ornaments of adult tropicbirds among the years 2000 - 2002, based on one set of measurements (at first capture) from each individual. Many of the birds measured ($n = 422$) had been banded as chicks and were of known age, so I was able to directly quantify age-related differences in ornaments. Using individuals measured during the incubation period, I regressed body mass on body size (the first principal component of a factor analysis of wing, tarsus and culmen lengths, Table 3.1). The transformation method for the factor analysis was Orthotran/Varimax. I used the residuals as indices of body condition for comparison with ornament expression (StatView 5.0). Allometric regressions were carried out for wing, culmen, and tarsus lengths as well as body condition using simple linear regression. I regressed fully grown streamer length on wing, culmen, and tarsus lengths as well as body condition. Estimates of slopes, intercepts, and confidence intervals are provided.

To examine the relationship of ornament expression to breeding stage, I identified male and female pair members and monitored nests in years 2000 ($n = 59$) and 2001 ($n = 44$). The female lays a single egg. Each nest was checked every two days to record status and pair member attendance. The date of laying, hatching, and fledging dates for each nest was also recorded. I calculated egg volume using the formula 0.512 x (egg length x 0.1) x ((egg width x 0.1) ^ 2) (Birkhead and Nettleship 1984). I used the egg volume index 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 the nearest gram). I used the asymptotic chick body mass at 58 days (the mean time to asymptote) for my analysis to explore the relationship of streamer length to body mass of chick. I examined if female ornament expression was influenced by her body condition index of the previous year. We examined if nest fate (egg failed, dead chick, or fledged chick) was influenced by ornament expression of parents. To examine the relationship between ornament expression of male and female pair members, I compared fully grown streamer lengths and the mean ratio of streamer lengths. 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 ten days or less of each other and used only once in the analysis unless from different years.

3.4 Results

Ornament measurement. — I captured and measured 241 male, 192 female, and 226 unknown sex individuals. Many birds were captured more than once in the same year (recaptured within year, RWI, n = 349), and some again in the next year (recaptured between years, RBY, n = 807). Repeatability of measurements within measurer (r_I, the intra-class correlation coefficient) was high (0.9-1.0) and measurement error (ME), the percent of total variability due to within-individual variation (Bailey and Byrnes 1990), was very low (0.08-0.23%; Table 3.2). I noted measurement asymmetry of fully grown tail streamer (a difference between left and right fully grown tail streamers) based on measurements of birds with two fully grown streamers; (mean = 47.8 ± 3.5 SE mm, range = 1.5–144.5). The asymmetries were attributable to wear of the older streamer. The mean wear rate of a fully grown streamer was 0.3 ± 0.03 SE mm day^{-1} (Chapter 2).

Table 3.1 Principal component factor analysis for measures of body size (n = 124).

	Unrotated factor 1
eigen value	1.27
percent variance	42.2
length of flattened wing	0.507
length of culmen	0.748
diagonal length of tarsus	0.670

Table 3.2 Measurement error and within-measurer repeatabilities of the Red-tailed Tropicbird ornament and wing measures.

Ornament	**ME (%)**[a]	r_I	**SE**	*F*	**df**	*P*
tail streamer length	0.08	1.0	-	0.000	302	0.98
wing length	0.23	0.9	-	0.001	241	0.97

[a]ME: 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).

Variation of ornament compared to other traits. — Fully grown tail streamers had higher coefficients of variation than non-ornamental traits (Table 3.3). 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 nearly constant. 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 3.4).

Table 3.3 Variation of ornaments and morphological traits of adult Red-tailed Tropicbirds in relation to gender.

	males			**females**				
Variable	**(mean ± SE, *n*)**	**CV(%)**	**SE for CV**	**(mean ± SE, *n*)**	**SE for CV**	**CV(%)**	**(m/f)**[a]	***t*, df, *P***
length of streamer (mm)	403.4 ± 2.9, 218	10.7	0.36	388.0 ± 3.3, 177	0.42	11.2	1.04	3.5, 393, 0.005[b]
length of flattened wing (mm)	324.6 ± 0.9, 62	2.2	0.13	323.8 ± 0.8, 63	0.11	1.8	1.00	0.7, 122, 0.5
length of culmen (mm)	62.4 ± 0.3, 62	3.6	0.24	61.3 ± 0.3, 63	0.21	3.5	1.02	2.8, 123, 0.005[b]
diagonal length of tarsus (mm)	28.2 ± 0.2, 61	4.3	0.28	27.9 ± 0.2, 63	0.30	4.6	1.01	1.1, 121, 0.3
(body mass)$^{1/3}$ (g)	218.7 ± 2.0, 62	7.2	0.46	220.2 ± 2.3, 63	0.51	8.2	1.00	0.5, 123, 0.6

[a] SD: Sexual dimorphism index (male trait size/female trait size).

[b] Significant differences at a tablewide *P*<0.05, using sequential Bonferroni analysis.

Table 3.4 Allometric relationships of body-size measures (mm) on fully grown streamer length (mm). Fully grown streamer length was regressed on body-size measures.

	Intercept (95% C.I)	**slope (95% C.I.)**	***n***	**r^2**	**P**
length of flattened wing (mm)	200.26 (-210.69, 611.2)	0.61 (-0.66, 1.88)	104	0.009	0.341
length of culmen (mm)	483.64 (274.06, 693.22)	-1.38 (-4.76, 2.00)	104	0.006	0.421
diagonal length of 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

Sexual dimorphism and ornament variability of males and females. — Patterns of variation were similar between the sexes (Table 3.3). Fully grown streamers of males were 4% longer than mean female fully grown tail streamers. This 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 streamers varied significantly across years in females but not in males (females: ANOVA, $F_{2,\,279} = 5.1$, $P = 0.01$; males: ANOVA, $F_{2,\,352} = 1.0$, $P = 0.4$; Figure 3.1). Based on 172 individuals with a fully grown streamer at initial capture in the first year and again at initial capture in subsequent years, there was a strong correlation with high repeatability ($r = 0.5$, $P < 0.0001$, $r_I = 1.0$; Figure 3.2). Based on 372 adults of known age (3–22 years old, mean = 9.6 yrs) I found no correlation between fully grown streamer length and age of individual ($r = 0.3$, $P = 0.6$; Figure 3.3). Ornament expression does not increase with age. There was no difference in ornament expression between males and females (unpaired $t = 0.2$, df = 209, $P = 0.8$).

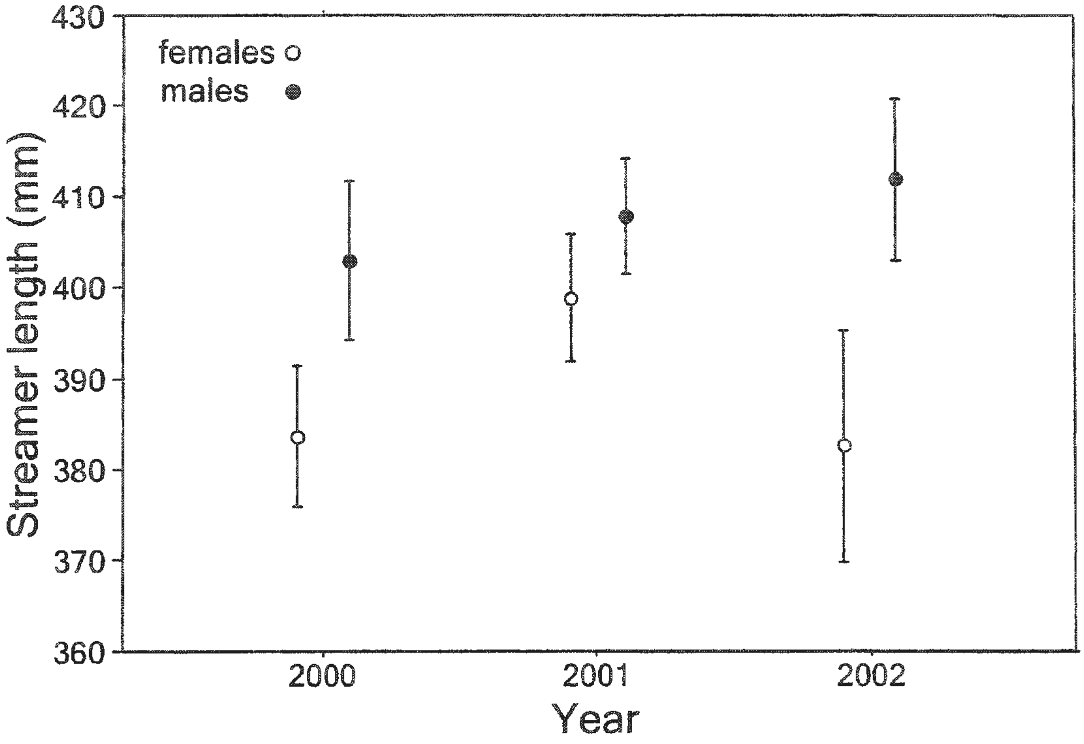

Figure 3.1 Variation in male and female fully grown tail streamer expression according to year at Tern Island, 2000—2002 (means = 95% confidence limits).

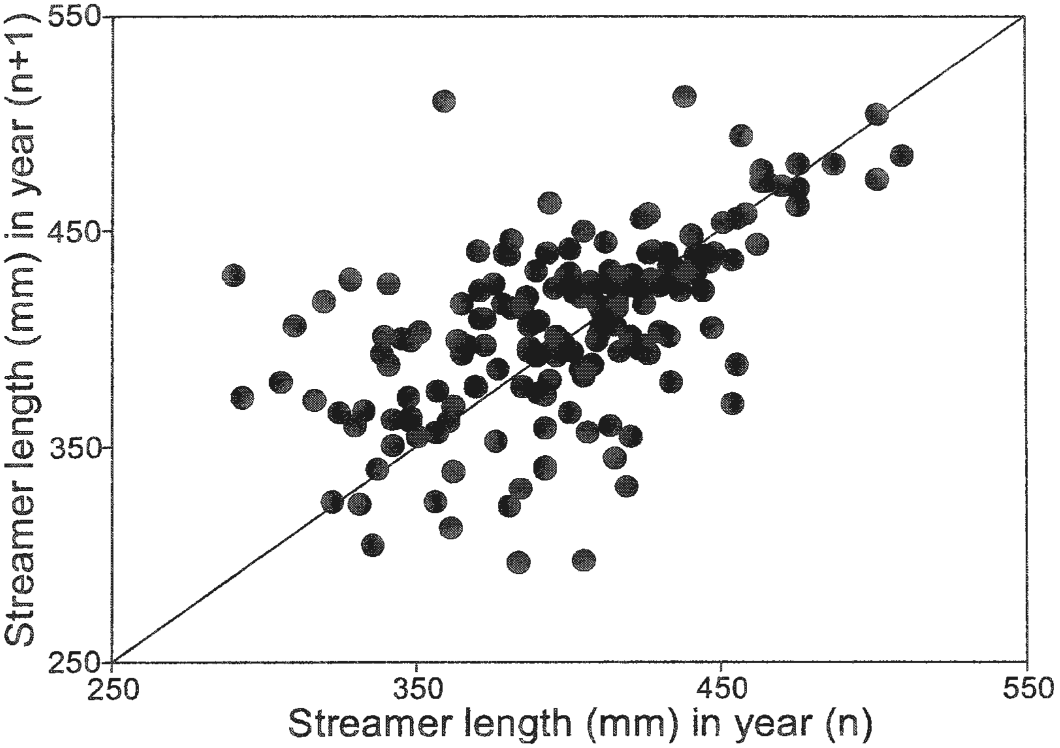

Figure 3.2 Plot of fully grown streamer length at first capture in year (n+1) versus length at first capture in year (n) of Red-tailed Tropicbirds, based on 172 individuals measured twice (line indicates 1:1, i.e. no change in ornament size).

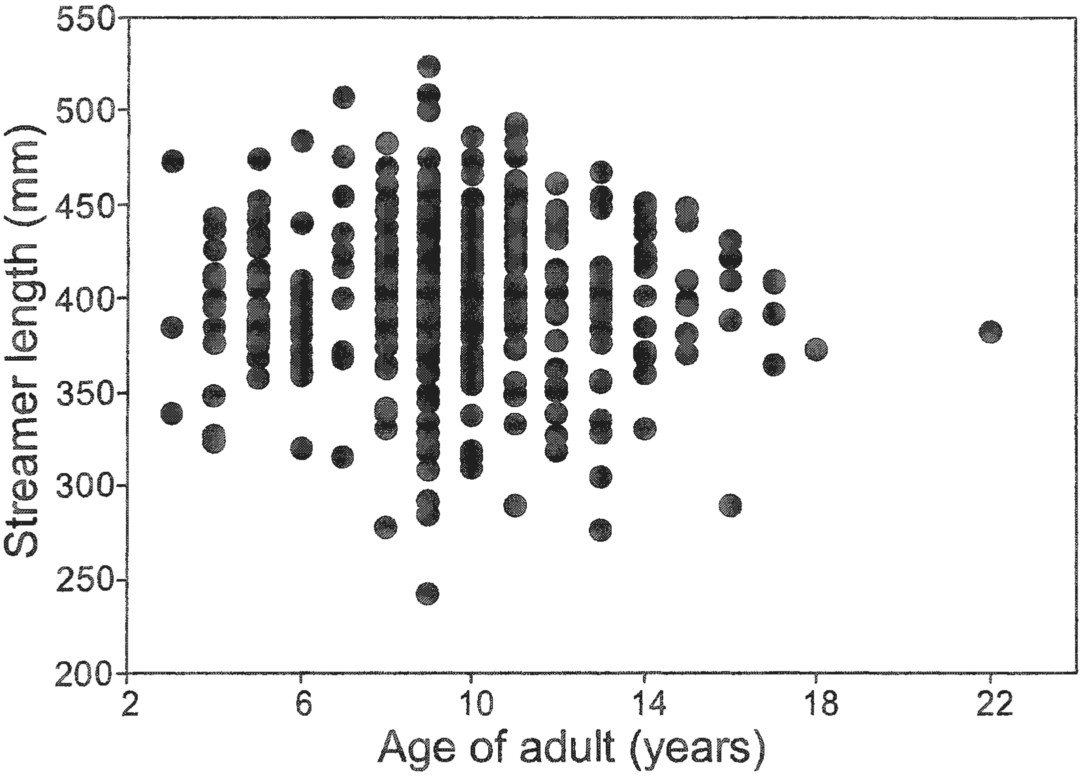

Figure 3.3 Plot of fully grown streamer length versus age versus of Red-tailed Tropicbirds, based on 372 individuals.

Covariation with ornaments and other traits. —Fully grown tail streamer length was not correlated with body size (PC1) ($r = 0.06$, df = 117, $P = 0.5$). There was no evidence for covariation of the tail streamer ornament with other morphological traits (wing, culmen, and tarsus) within individuals, except for a weak negative correlation between female fully grown streamer length and culmen length (Table 3.5).

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, $P = 0.7$; Figure 3.4). No relationship was found between fully grown streamer length and body condition of the previous year (female; $r = 0.02$, df = 44, $P = 0.9$; male; $r = 0.1$, df = 29, $P = 0.5$) nor between the lay date of an individual and streamer length ($r = 0.1$, df = 151, $P = 0.5$). 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, $P = 0.6$) nor with individuals with failed eggs before hatching (unpaired $t = 0.6$, df = 49, $P = 0.5$). Finally, I investigated the relationship between the fully grown streamer length of male and female pair members and the asymptotic body mass of their chick. We found no significant correlations (male; $r = 0.6$, df = 8, $P = 0.09$; female $r = 0.3$, df = 11, $P = 0.3$; Figure 3.5).

Table 3.5 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).

	length of flattened wing (mm)	**length of culmen (mm)**	**diagonal length of tarsus (mm)**	**length of streamer (mm)**
length of flattened wing (mm)	1.00	0.081	0.090	0.009
length of culmen (mm)	0.056	1.00	0.113	-0.042
diagonal length of tarsus (mm)	0.091	0.265	1.00	0.211
length of streamer (mm)	0.093	-0.273*	-0.117	1.00

*Significant differences at a tablewide $P<0.05$, using sequential Bonferroni analysis.

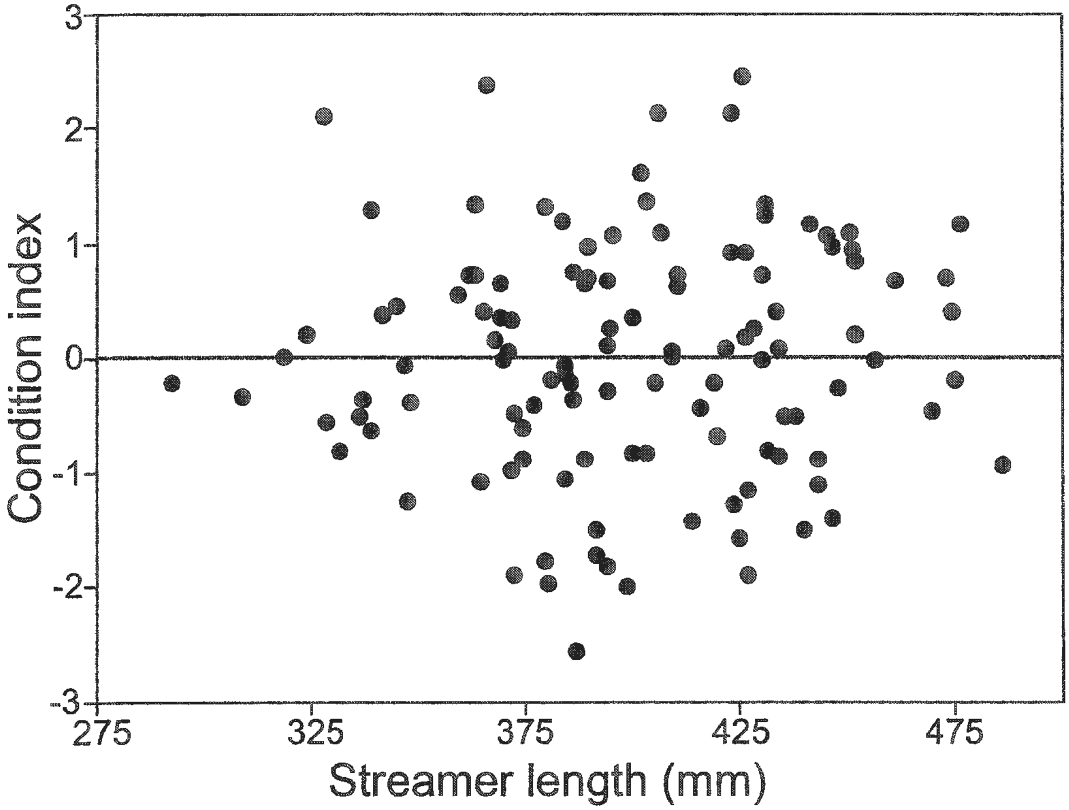

Figure 3.4 The relationship between condition index and fully grown streamer length of Red-tailed Tropicbirds. There was no significant relationship.

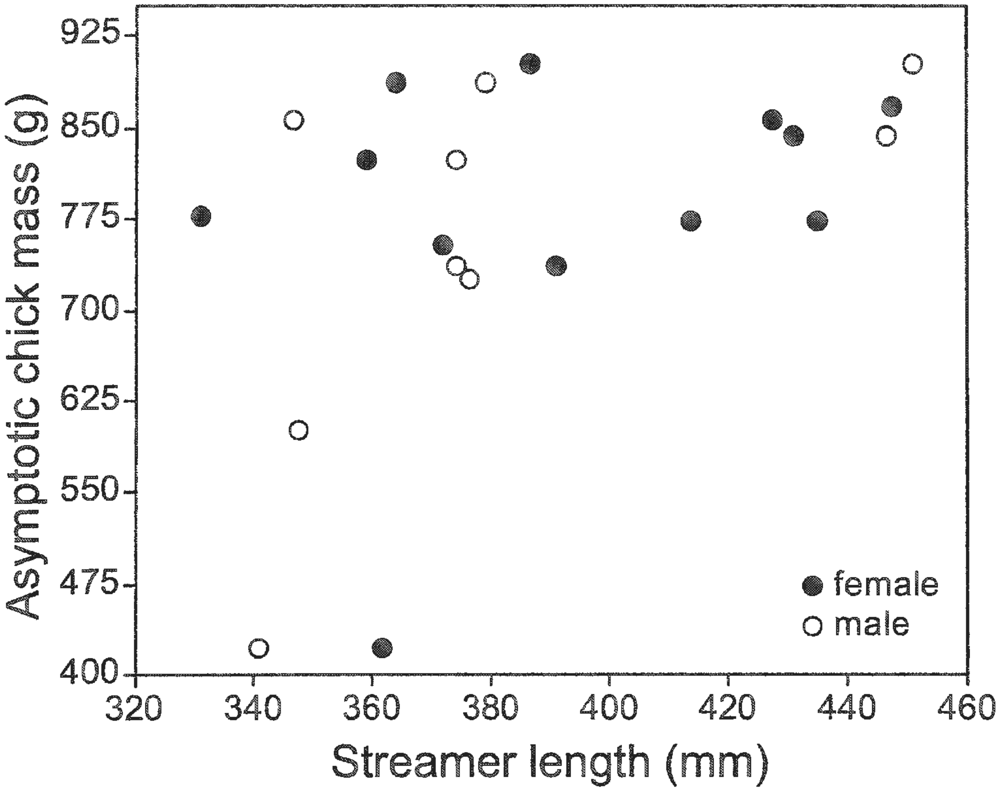

Figure 3.5 The relationship of asymptotic chick body mass to fully grown streamer length of parents.

Evidence for assortative mating. — No correlation was found between the fully grown tail streamer length of male and female pair members ($r = 0.2$, df = 56, $P = 0.3$). However, a correlation was found between the ratio of the lengths of the two streamers (growing streamer vs. fully grown streamer) of pair members ($r = 0.5$, df = 35, $P = 0.01$; Figure 3.6), suggesting that individuals paired with mates with similar tail streamer symmetry as determined by stage of growth.

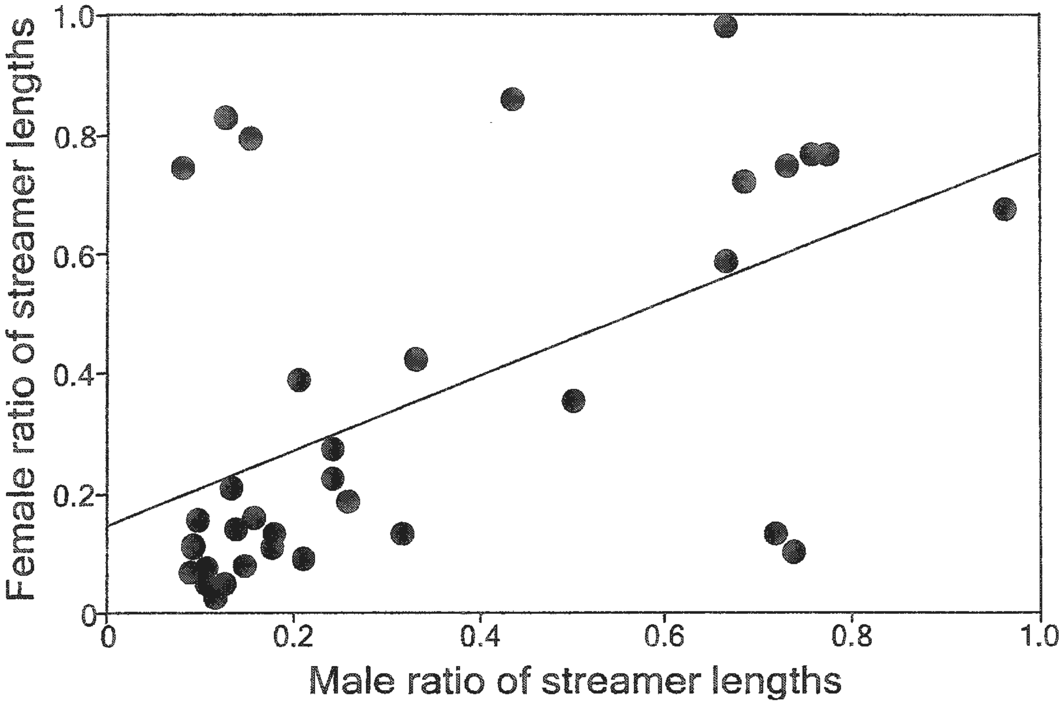

Figure 3.6 Regression plot of male pair member ratio of streamer lengths versus female pair member ratio of streamer lengths in Red-tailed Tropicbirds. Ratios close to 1.0 are long growing streamers nearly fully grown, ratios < 0.5 are streamers beginning to grow. Pairs have streamers of similar symmetry.

3.5 Discussion

Fully grown tail streamers of Red-tailed Tropicbirds' exhibited measurement asymmetries (the difference between left and right fully grown tail streamer) of up to 144 mm due to wear at the tip of the older streamer. This wear accounted for most of the difference in lengths of fully grown streamers in individual birds.

Both male and female tail streamers were more variable (higher coefficients of variation) than the non-ornamental morphological traits such as culmen, wing, and tarsus lengths. Analyzing variation in the length of similar tail ornaments in birds, Alatalo et al. (1988) found that tail length varied much more than other body size characters within populations. Thus, the general pattern of variation of Red-tailed Tropicbird tail streamers measured in my study closely matched that of other sexually selected ornaments.

Ornamental expression was similar between sexes except in streamer length, which was 4% longer in males. The expression of ornaments in females was unlikely a simple result of genetic correlation between sexes (e.g., Lande and Arnold 1985). In some monogamous species, long tail ornaments have evolved in both sexes and may signal breeding experience and parental ability (Cramp and Simmons 1983). This idea predicts that long tail ornaments in both sexes should occur mainly in species with biparental care, and that degree of similarity of the tail males and females should be correlated with similarity in their parental roles (Andersson 1994). The equally-shared parental care of Red-tailed Tropicbirds agrees with this prediction. Growing evidence suggests a role for mutual sexual selection favoring male and female ornaments (Hill 1993, Jones and Hunter 1993, Amundsen et al. 1997, Jones and Hunter 1999) and mutual preferences for plumage color (Burley 1977, Burley and Moran 1979). Males' greater ornament expression and slightly larger overall body size may be explained by higher mating success benefits, or differences between males and females in ability to produce an ornament, or differences between sexes in costs of mate choice (Johnstone et al. 1996).

A significant correlation and high repeatability was found with individuals' tail streamer ornaments among years indicating streamers grow to a similar final length each year. There was no evidence that ornament expression changed with age (3-22 years). This may indicate that Red-tailed Tropicbirds streamer length may not be a good indicator of quality based on an individual's previous experience. Andersson (1971, 1976) found that the central two tail streamers of the Long-tailed Skua (*Stercorarius longicaudus*) used in courtship display by both sexes appeared to increase in length with age. My results were more similar to those of previous studies of Crested Auklet (*Aethia cristatella*) and Least Auklet (*Aethia pusilla*) sexually monomorphic feather ornaments (Jones and Montgomerie 1992, Jones et al. 2000) which are extravagant but cheap to produce and apparently arbitrary in expression which suggests the ornaments were unreliable viability indicators.

Streamer length, although highly variable across individuals, had no relationship with other structures important to flight such as body size (PC1) or wing length among the 103 individuals measured. Thus, it appears that tropicbird tail streamer ornaments do not have a beneficial aerodynamic function.

The tail streamers consist of bright red carotenoid, melanin pigments, and structural keratin amounting to less than a gram on a bird averaging about 700 g in body mass. An individual's slender profile is unlikely to generate significant aerodynamic drag (Thomas 1993), so energetic costs of streamer production and display are assumed to be small. However, unlike 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, Chapter 2), consistent with them being a (a) costly trait that can only be developed only over a long period or (b) a trait that provides little benefit. Nevertheless, I 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), making Red-tailed Tropicbird tail streamers a possible case of an indicator function (Andersson 1982). However, I found no evidence that tail streamer ornaments are correlated with measures of individual vigour. I found no correlation between ornament size and body condition index, suggesting that Red-tailed Tropicbird tail streamer ornaments are not signals of individual condition. The condition index was based on mass during the 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 due to 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 the hematocrit, the proportion of blood volume occupied by packed red blood cells (Carpenter 1975). Saino et al. (1997) found hematocrit to be a useful measure of individual's quality, finding significant correlations with Barn Swallow (*Hirundo rustica*) 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, however further data are required to confirm a possible relationship. In a study by Johnsen et al. (1996) female epaulet color in red-winged blackbirds was influenced by female condition of the previous year. I did not find this to be the case with female tropicbirds; streamer length was not influenced by female condition of the previous year. The data are more consistent with the hypothesis that the evolutionary origin of the tail streamer is a result of a runaway or sensory exploitation mechanism than as viability indicators.

There was some contradictory evidence related to assortative mating; 1) no correlation between the streamer lengths of male and female pair members ($n = 57$), suggesting that length of a fully grown streamer was not a sole determining factor in mate choice and 2) a correlation between the ratio of streamer lengths (growing streamer vs. fully grown streamer) of pair members measured within ten days and less of each other, indicating that ornament growth is 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. These findings suggest that the symmetry of streamers is an important optical signal. To confirm the role of sexual selection in favoring tropicbird ornaments I require field experiments to assess the effect of manipulations of male and female streamer length on their mating success.

Taken together, my findings strongly suggest that the 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 of the year-round possession of at least one streamer, 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 other display traits (i.e. soft parts, plumage, and vocalizations) and communicative behavior.

3.6 Acknowledgments

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Chapter 4

Summary

Ornate feather structures are displayed by a variety of bird species. These ornaments vary in expression between sexes, across age classes, and among individuals (Andersson 1994). In the Red-tailed Tropicbird, a socially monogamous seabird, males and females possess elongated tail streamer ornaments. The two streamers are bilaterally symmetrical and bright red in color. Sexes are monomorphic and commonly return to the same nest site and mate each year. As part of their sexual behavior, tropicbirds perform highly complex and elaborate aerial displays with members of the opposite sex above potential nest sites. They were an ideal species to investigate ornament function and the mechanism responsible for ornament evolution.

Tail streamer ornaments were studied over three years. Adults were marked for individual identification (many banded as chicks). To determine the sex of an individual a simple method for molecular sexing (Fridolfsson and Ellegren 1999) or cloacal examination near laying was used. Ideally, tail streamers would have been measured over an entire year to determine the patterns of growth and molt, however year-round data collection was not possible because individuals are at sea during the non-breeding season (August –December). I was able to collect data over seven months (January – July) resulting in a very comprehensive dataset with many known sex and known age individuals. Tropicbird ornaments consist of two bright red elongated central tail feathers averaging 400mm in length when fully grown (Chapter 2). The two streamers grow alternately, so each adult possesses one fully grown streamer year round (except in cases of breakage) with the other one usually growing (Chapter 2). Streamer growth rate is approximately 2mm/day, declining as the streamer approaches its final length (Chapter

2). This long and flexible bright red feather takes a very long time to grow (about a half a year). Once a streamer has reached a final length it is then retained for another half a year, at which point the streamer is dropped in the colony or at sea. It is a common to find molted streamers on the ground at or around the nest site as observed by the author. Within approximately a week, a new replacement feather emerges and begins to grow (Chapter 2).

I found that ornament expression was timed with the breeding season. The tropicbird breeding season begins in February with the arrival of adults and egg laying peaks in late March with chick rearing into August. A tropicbird arriving at the colony in the beginning of the season has two fully grown tail streamers (or one is fully grown and the other nearly fully grown), both in excellent condition. Within a month of laying, one of the streamers (the oldest of the two, if both are fully grown) drops and a new one begins to grow. The streamer grows throughout the chick rearing period until it reaches a full length again in August/September (Chapter 2). The seasonal trend suggests it is important for a bird to arrive at the breeding colony with both streamers as long as possible. I investigated ornament expression in male and female pair members monitored during two breeding seasons. I found a significant correlation between the ratio of streamer length (growing vs. fully grown) of male and female pair members. The symmetry of the streamers may act as a optical signal and perhaps signal a readiness to breed suggesting that streamers are a sexually selected trait (Chapter 2).

Tail streamers appear to have no significant aerodynamic function related to tropicbird flight (Chapter 3). I found no relationship between the length of a fully grown streamer and wing length or body size (PC1). I predicted that if tail streamers have a significant flight function, they should correlate with other aerodynamically important traits such as wing length or body size across individuals (discuss aerodynamic studies). Streamers showed high levels of variability in expression similar to the costly sexually selected ornaments of other bird species (Alatalo et al. 1988). Tail streamers do not appear to be a good indicator of an individual's quality or breeding productivity (traits examined e.g. body condition index, timing of breeding, egg size, chick asymptotic body mass, and nest fate). The expression of the ornament seems to be arbitrary. In 2001, I attempted to repeat the classic tail manipulation protocol (Møller 1988) and experimentally test whether mating preferences focus on male and female tail streamer length. Using superglue, I lengthened the streamers on 22 females (study birds) with an additional feather length of 80 mm cut from molted streamers found in the colony. However, due to difficulties with the attachment process of the additional feather length the data were not analyzed. The sexual selection hypothesis predicts that individuals with longer streamers will obtain mates faster and generally be more attractive to the opposite sex. The evolutionary origin of the streamer appears to be the result of a runaway or sensory exploitation mechanism rather than a viability indicator (Chapter 3). The sexual behavior of tropicbirds and use of tail streamers in aerial displays with members of the opposite sex offers strong support for an ornamental function. Further research is necessary to investigate the role of mutual sexual selection involving mutual mating preferences that hypothetically favor tropicbird tail streamers.

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