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Tail length and sexual selection in a monogamous, monomorphic species, the Roseate Tern *Sterna dougallii*

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Patricia Szczys

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Abstract Both male and female Roseate Terns (*Sterna dougallii*) have unusually long outer tail feathers, and males tend to have longer tails than females. We examined whether these tail streamers may have evolved as a result of sexual selection, using data from a 15-year study at Bird Island, Massachusetts, USA. Data on tail length were analyzed for 2,515 terns, of which 745 were of known sex. Tail length was positively correlated with predictors of reproductive success, such as laying date, body mass, and age, and thus can act as an indicator of mate quality. The increase in mean tail length with age appeared to result from a combination of growth in relatively young terns and differential survival among older terns. The mean duration of pair bonds was short at 1.73 years. A female-biased sex

ratio is present in this population, and we demonstrated that short-tailed females are not preferred mates: females paired to males had longer tails than those in female–female pairs or other multi-female associations. In male–female pairs, tail lengths of mates were correlated, but this may have resulted in part from the correlation in ages. These observations are consistent with the hypothesis that tail streamers are used by both sexes in mate choice. In contrast to our results for tail length, tail symmetry was not significantly related to indices of individual quality and was not significantly correlated between mates.

Keywords Female–female pair · Fluctuating asymmetry · Sexual selection · *Sterna dougallii* · Tail length

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B. G. Palestis (✉)
Department of Biological Sciences, Wagner College,
1 Campus Road, Staten Island, NY 10301, USA
e-mail: bpalesti@wagner.edu

I. C. T. Nisbet
I.C.T. Nisbet & Company, North Falmouth, MA, USA

J. J. Hatch
University of Massachusetts, Harbor Campus, Boston, MA, USA

Present Address:
J. J. Hatch
Lower Dibbe, South Tawton, Devon EX20 2LQ, UK

J. M. Arnold
Pennsylvania State University, Berks Campus,
Reading, PA, USA

P. Szczys
Eastern Connecticut State University,
Willimantic, CT, USA

Zusammenfassung

Schwanzlänge und sexuelle Selektion in der monogamen und monomorphen Rosenseeschwalbe *Sterna dougallii*

Männliche wie weibliche Rosenseeschwalben (*Sterna dougallii*) haben ungewöhnlich lange äußere Schwanzfedern, wobei die der Männchen normalerweise noch länger sind. Anhand der Daten einer 15-jährigen Studie auf Bird Island in Massachusetts (USA) untersuchten wir, ob diese Schwanzfedern aufgrund sexueller Selektion entstanden. Wir untersuchten die Schwanzlängen von 2,515 Seeschwalben, wobei 745 bekannten Geschlechts waren. Schwanzlänge war positiv korreliert mit Variablen, die den Reproduktionserfolg beeinflussen (Legedatum, Körpermasse, Alter), und könnte daher als Anzeichen für die Qualität des Brutpartners verwendet werden. Das Wachstum junger Seeschwalben und ungleiche Überlebensraten älterer Individuen schien die Verlängerung der Schwanzfedern mit dem Alter zu bedingen. Die mittlere

Dauer einer Paarbindung war 1,73 Jahre. In der Studienpopulation war ein Weibchenüberschuss gegeben und wir fanden, dass kurzschwänzige Weibchen nicht die bevorzugten Partner waren: Weibchen, die mit Männchen verpaart waren, hatten längere Schwanzfedern, als solche in Paaren von zwei Weibchen oder anderen Weibchenverbänden. In Männchen-Weibchen Paaren waren die Schwanzlängen der Partner korreliert, aber das mag zum Teil an der Korrelation der Alter von Paarpartnern gelegen haben. Diese Beobachtungen stimmen mit der Vermutung überein, dass die Länge der Schwanzfedern von beiden Geschlechtern in der Partnerwahl berücksichtigt wird. Entgegen der Ergebnisse für Schwanzlänge war die Symmetrie der Schwanzfedern kein Indiz für individuelle Qualität und war zwischen Partnern nicht signifikant korreliert.

Introduction

Research on the evolution of ornamental traits by sexual selection has focused on the evolution of large or colorful traits in the males of polygynous species, such as the Long-tailed Widowbird (*Euplectes progne*; Andersson 1982). Darwin (1871) and Fisher (1930) proposed that males in monogamous species may also benefit from elaborate traits if such traits allow them to pair earlier in the breeding season and/or to obtain more fecund mates. This hypothesis has received both empirical and theoretical support (O'Donald 1980; Møller 1988; Kirkpatrick et al. 1990; Evans and Hatchwell 1992; Regosin and Pruett-Jones 2001). However, there is increasing awareness that females of many species are also ornamented (Amundsen 2000; Kraaijeveld et al. 2007; Clutton-Brock 2009; Martinez-Padilla et al. 2011). The presence of ornaments in both sexes could result from a genetic correlation between sexes, with female ornamentation a nonadaptive byproduct of male ornamentation (Lande 1980), but could also result from mutual mate choice, with sexual selection favoring the evolution of ornaments in both sexes (see below).

Preferences for traits like long tails can arise if the choice results in direct benefits, indirect (genetic) benefits, or Fisherian runaway selection (Andersson 1994). In species like terns, where resources such as parental care and courtship feeding are provided, the benefits of mate choice may result more from direct effects of mate quality on fecundity and offspring survival than from indirect genetic benefits to offspring (Maynard Smith 1991). Individual quality can be displayed not only by tail length but also by tail symmetry, as fluctuating asymmetry (FA) results from the inability of individuals to overcome environmental or genetic stresses that occur during development (Møller and Swaddle 1997).

Most monogamous seabirds lack obvious sexual ornaments, but some species have conspicuous structures such as long tails or brightly colored bills, feathers, or wattles. Among terns, examples include the moustache and wattles of Inca Terns (*Larosterna inca*, Velando et al. 2001), bill tip color in Arctic Terns (*Sterna paradisaea*; Møller et al. 2007), and ultraviolet reflectance marking freshly-molted wing feathers in Common Terns (*S. hirundo*; Bridge and Nisbet 2004; Bridge and Eaton 2005). There appears to be variation among seabird species in whether ornaments are indicators of individual quality or arbitrary signals (Veit and Jones 2003). We examined whether sexual selection has driven the evolution of tail length and/or symmetry in the Roseate Tern (*Sterna dougallii*). The Roseate Tern is a long-lived, monogamous, colonially nesting seabird with biparental care (Gochfeld et al. 1998), and is an endangered species in the USA and Canada (US FWS 1987). The present study of the long-tailed Roseate Tern is unavoidably non-experimental and therefore must be interpreted with caution. The results of experimental and correlational studies of tail length and other potential ornaments can be quite different (Cuervo et al. 1996). In addition, tail length in 1 year may have delayed effects on reproductive success if parental investment is adjusted to compensate for the costs of long tails (Cuervo et al. 2003).

Terns generally have forked tails and some have been known for this reason as “sea swallows”. The aerodynamic function of the fork is particularly associated with enhancing agility and maneuverability (Thomas and Balmford 1995). However, the depth of the fork differs markedly among species and forks longer than the aerodynamic optimum may result from sexual selection (Thomas and Balmford 1995). In adult Roseate Terns, the distal part of the tapering outermost rectrix (t6), the tail “streamer”, has very narrow vanes. At rest, these tail streamers extend well beyond the wing-tips. These are quite flexible and, in some forms of flight, including courtship flight, they flutter conspicuously behind the bird (personal observation). Three tern species, similar in size, that have unusually long tails are the Roseate, Arctic, and White-fronted (*S. striata*) Terns. Of these, the Roseate has relatively short wings and the tail/wing ratio is 0.76–0.80 for males, compared to 0.64–0.66 in the other long-tailed species, and as low as 0.4 in other terns (Cramp and Simmons 2004; Gochfeld et al. 1998; Higgins and Davies 1996). In Barn Swallows (*Hirundo rustica*), the subject of extensive work on deeply-forked tails (e.g., Møller 1988; Cuervo et al. 1996, 2003), the ratio is 0.83 (Cramp and Simmons 2004).

Prior to forming the pair bond, Roseate Terns perform an elaborate flight display with potential mates (Gochfeld et al. 1998; Cramp and Simmons 2004). This display is characterized by several birds circling upward at high speeds: the first two birds to reach the highest point in the

ascent display together during the descent (Gochfeld et al. 1998). Such strenuous flights, in which the tail streamers are conspicuous, may demonstrate maneuverability and condition. The tail streamers are also raised prominently in ground displays during pair formation (Cramp and Simmons 2004).

Because Roseate Terns are monogamous with biparental care (Gochfeld et al. 1998), it is predicted that mutual mate choice should occur (Trivers 1972; Jones and Hunter 1993; Amundsen 2000; Kokko and Johnstone 2002; Kraaijeveld et al. 2007; Rowe and Weatherhead 2011). Choosiness by both sexes should result in assortative mating by mate quality (Parker 1983), and, if ornaments are present, they should be observed in both sexes (Johnson and Burley 1997; Kraaijeveld et al. 2007). Species in which ornaments are restricted to males, on the other hand, tend to be those in which males contribute little to parental care (Winqvist and Lemon 1994; Cuervo and Møller 2000). Assortative mating (in the broad sense of correlation between mates in one or more traits) has been reported in the Common Tern (Coulter 1986; Wendeln 1997; Bridge and Nisbet 2004; Ludwig and Becker 2008; but see Nisbet et al. 2007), although assortative mating alone does not necessarily imply mate choice in a species with long-term pair bonds (Bridge and Nisbet 2004; Ludwig and Becker 2008). The only previous data on mate retention in Roseate Terns were those of Nisbet et al. (1998), who reported only the mean duration of pair-bonds in pairs that remained together for at least 2 years, without reporting the number of pairs that were together for only 1 year.

Although mutual mate choice is expected in Roseate Terns and the sexes look identical to human observers, the strength of sexual selection is probably not equal in males and females and subtle sexual dimorphism is present. In most terns, including Roseate Terns (Gochfeld et al. 1998; Palestis et al. *in press*), males are slightly larger than females (Coulter 1986; Devlin et al. 2004; Nisbet et al. 2007; Shealer and Cleary 2007) and take a leading role in courtship displays, including feeding the females during egg-laying (González-Solís et al. 2001; Cramp and Simmons 2004). Although there is substantial overlap in tail length among the two sexes, male Roseate Terns tend to have longer tails than do females (Gochfeld et al. 1998). Roseate Terns in the northwest Atlantic population show a female-biased sex ratio and the presence of female–female pairs or other multi-female associations with low reproductive success (Nisbet and Hatch 1999). At the colony studied here, approximately 20 % of females did not have male mates (Nisbet and Hatch 1999). Therefore sexual selection is expected to act more strongly on females in this population than would otherwise be predicted (Andersson 1994; Kvarnemo and Ahnesjö 1996; Rosvall 2011). Data on laying date, clutch size, and egg size all suggest that females paired with females are of low phenotypic quality

(Nisbet and Hatch 1999), and therefore imply that males are choosy in selecting mates. However, at least part of these differences among females may result from a lack of courtship feeding in female–female pairs.

We predicted that if tail streamers function as sexual ornaments in Roseate Terns, then the terns should mate assortatively by tail length and/or FA and females in female–female pairs should have shorter and/or more asymmetrical tails than those paired to males. To function as indicator traits, tail characteristics should also be correlated with other predictors of reproductive success (Andersson 1994; Veit and Jones 2003), such as laying date and age (Burger et al. 1996; Arnold et al. 2004).

Methods

Study site

This study was conducted at Bird Island, Buzzards Bay, Massachusetts (41°40'N, 70°43'W) in 1987–2000 and 2009. Roseate Terns have been studied at this site since 1970. In recent years, 500–900 pairs have nested on the island and about one-third of these are of known age based on banding as nestlings. Roseate Terns nest under dense vegetation and in nest boxes, but conduct ground displays in the open on rocks and other raised objects.

Data collection

Roseate Terns were trapped randomly throughout the colony site, except that in 1992–1994 trapping was focused on birds thought to be in multi-female associations (Nisbet and Hatch 1999). Terns were trapped on their nests after ≥ 15 days of incubation using walk-in traps placed over the nest. The date on which the first egg was laid (hereafter, laying date) was determined or estimated for each nest from observations at the time of laying and/or hatching. Several measurements were taken, including head length (from the back of the skull to the tip of the bill), wing length, body mass, and tail length. Handling time did not exceed 5 min. Tail length on both sides of the tail was measured to the nearest mm from the point of insertion of the central feathers (determined by pushing a metal ruler to the point of resistance) to the tip of the outermost tail feather. If one of these feathers was broken or worn, it was not measured, and in some cases one was missing. Identification of a broken feather was unequivocal if it ended in a distinct “v” formed by the vanes, but vanes are less prevalent at the ends of long tail streamers than on other feathers, and it is possible that there were damaged tail feathers that were overlooked.

As a single overall index of body size, we used the first principal component (PC1) from a principal component

analysis (PCA) of head length, wing length, and body mass, after standardizing these body size variables for sex by subtracting the mean values for the appropriate sex. The PCA was performed with Factor Analysis in SPSS 12.0 (SPSS, 2003), using the principal components extraction method on the correlation matrix. PC1 was strongly positively correlated with all three body size variables; the strongest correlation was with head length (see “Results”). PC1 had an eigenvalue of 1.44 and was the only principal component with an eigenvalue greater than one. Because only one component was extracted, the solution was not rotated.

We do not have measures of reproductive success for most birds in this study, but laying date is negatively correlated with reproductive success in Roseate Terns (Burger et al. 1996) and is an indicator of parental quality in other terns (Arnold et al. 2004). In this study, therefore, we use laying date as a proxy for individual quality (early laying dates indicating high quality), and test whether tail length is correlated with this and/or other characteristics of individual birds such as body size and age.

Measurements were taken by ICTN. and JJH. in 1987–2000, and in 2009 by ICTN. and BGP. (tails) and Jeffrey Spendelow (other measurements). We checked for repeatability (Lessells and Boag 1987) and the presence of significant FA (see below) by measuring each tail streamer twice per bird in 2009, in the following pattern: left, right, left, right. Repeatability of tail measurements was very high at $r = 0.996$ for both the right and left sides of the tail (right: $F_{238,241} = 560.5$, $p < 0.0001$; left: $F_{243,246} = 483.4$, $p < 0.0001$; differing degrees of freedom reflect individuals with missing or broken tail feathers on one side). In a subsample of birds measured by both observers, inter-observer concordance was very high ($r = 0.995$, $n = 6$, $p < 0.0001$).

A total of 670 birds were sexed in 1987–2000 using molecular markers (Sabo et al. 1994; Szczyz et al. 2001). In addition, mates of birds known to be male by molecular sexing were assumed to be female ($n = 75$). The presence of multi-female associations, such as female–female pairs or males mated to more than one female, means that mates of females cannot be assumed to be males. In addition to molecular sexing, multi-female associations were also identified by the presence of supernormal clutches (>2 eggs) or by the presence of two eggs laid ≤ 1 day apart (Nisbet and Hatch 1999). Nisbet and Hatch (1999) estimated the sex ratio at this colony at 1.27 females to 1 male. Approximately 11 % of clutches were attended by female–female pairs and 1 % by other multi-female associations.

Statistical methods

Approximately 85 % of the birds studied were measured in only 1 year. If the same individual was measured in more

than 1 year, then only one encounter per individual or pair was used to eliminate non-independent data, except when examining within-individual changes in tail length and symmetry across years. Selection of encounters was random, except that encounters with complete measurements and/or at the extremes of the age distribution were preferred where available; otherwise we would not have had sufficient numbers of very young and very old breeders to examine variation with age. Three FA outliers well beyond the frequency distribution were removed, as recommended by Palmer (1994) and Palmer and Strobeck (2003). These were not known-sex individuals, so they would have been excluded from most comparisons regardless of being outliers.

After restricting the dataset, the sample included 2,515 terns with at least one outer tail feather (tail streamer) measured. If both were measured then the mean was used as “tail length” and if only one was measured then that value was used. Most of the comparisons depend on individuals being of known sex ($n = 745$). Many analyses also require individuals to be of known age, and/or to have other measurements in addition to tail length, and/or to have mates with known characteristics; thus, sample sizes in statistical comparisons are usually large but less than 745.

Laying date was standardized for year-to-year variation by subtracting the earliest recorded laying date in each year and was then square-root transformed for normality. Age was \ln transformed. Because of the lack of a clear correlation between tail FA and tail length and significant differences in tail length among groups (see “Results”), we do not correct FA for trait size (Palmer 1994; Palmer and Strobeck 2003).

Most analyses were performed using SPSS 12.0 (SPSS, 2003). FA was assessed using the Excel template at (<http://www.biology.ualberta.ca/palmer/asym/FA/FA-Refs.htm#tools>). All significance tests were two-tailed with an alpha level of 0.05, and, whenever appropriate, effect sizes are given in addition to p values. We used parametric tests except in the case of correlations involving FA. Here, we used the nonparametric Spearman Rank Correlation, as recommended by Palmer and Strobeck (2003), because of the sensitivity of Pearson correlations to unequal variances and extreme values and the presence of leptokurtosis in the frequency distribution of FA.

Differences between groups and correlations among traits were examined using t tests and Pearson correlation coefficients. To control for covariates, additional analyses were performed on subsets of the data using General Linear Models with Type III Sum of Squares. There was no significant year effect (year as random factor in General Linear Mixed Models, Wald $Z = 0.46$, $p = 0.65$ for known-age terns; Wald $Z = 0.27$, $p = 0.79$ for all terns),

so we do not include year as a variable in the analyses reported below.

We used linear regression to test for relationships between tail length and age in cross-sectional comparisons (one case per bird), analyzing both sexes together with ANCOVA. (No significant quadratic term was present and only linear regression results are reported here.) To test whether the cross-sectional relationships resulted from growth or from selection, we also analyzed data longitudinally. Among birds of known sex and known age that were measured in more than 1 year, we regressed $(t_{ij} - t_{ik})$ on $(y_j - y_k)$, where t_{ij} and t_{ik} are the tail lengths of bird i in years y_j and y_k . A positive regression coefficient would indicate growth within individual birds, with the slope equal to the mean rate of growth. Because growth might occur only in relatively young birds, we calculated regression coefficients separately for birds with ages ≤ 6 years ($n = 40$) and ≥ 6 years ($n = 41$) in both years y_j and y_k ; no bird was included in both groups. To compare these slopes with that observed in the cross-sectional analysis, we recalculated the latter after excluding the birds included in the longitudinal analysis, combining sexes because most birds in the longitudinal analysis were of unknown sex.

To test for assortative mating by age, we calculated the Pearson correlation coefficient between the ages of mates. To assess the contribution of mate retention to this probability, we compiled all cases in which a bird was paired with another banded individual and was encountered with the

same or another banded individual after an interval of n years. For individuals that were so encountered more than once, we used only the shorter intervals. For all cases in which $n = 1$, we determined the frequency of retaining the same mate in the next year. For the entire dataset, we used logistic regression to estimate $p(n)$, the probability that the focal bird would have the same mate after n years, and we used the regression equation to estimate the mean duration of pair bonds. Cases in which both members of a pair (or two members of a trio) met these criteria were counted twice in this analysis, because our interest was in individual birds rather than pairs. We used multiple logistic regression to determine whether $p(n)$ varied with the age of the focal bird. Correlations in tail length among mates were controlled for laying date or “pair age” in multiple regression. Pair age is the mean age of mates in a pair or the age of one member of the pair if only one is of known age (Nisbet et al. 2007).

Results

Tail length

Male Roseate Terns had 5.4 % longer tails than did females (Table 1; $t_{743} = 10.27$, $p < 0.0001$, Cohen's $d = 0.73$), and females paired to males (FM) had 2.1 % longer tails than females in multi-female associations (FF) (Table 1; $t_{373} = 2.94$, $p = 0.003$, $d = 0.30$). Comparisons between

Table 1 Morphological measurements (mean \pm SD) of Roseate Terns (*Sterna dougallii*) are shown for length of tail streamers (mm), tail streamer asymmetry (mm), head length (mm), wing length (mm), and body mass (g), across the following categories: females

mated to males (FM), females in multi-female associations (FF), females with mates of unknown sex (F?), males mated monogamously to females (MF), males in multi-female association (MFF)

Category	Tail length	Tail FA	Head	Wing	Mass
FM	176.0 \pm 12.0	4.3 \pm 5.2	77.0 \pm 1.4	227.5 \pm 4.5	114.0 \pm 6.4
	134–211 (217)	0–52 (185)	73.4–81.1 (214)	212–238 (206)	96–134 (209)
FF	172.4 \pm 11.3	4.7 \pm 5.2	76.8 \pm 1.5	227.5 \pm 4.9	112.1 \pm 6.6
	134–201 (158)	0–38 (129)	71.9–82.5 (158)	215–242 (156)	92–130 (153)
F?	176.0 \pm 11.8	5.4 \pm 5.8	77.0 \pm 1.6	227.8 \pm 4.8	113.0 \pm 6.5
	146.5–204 (98)	0–31 (85)	72.7–81.2 (94)	215–240 (93)	95–129 (94)
All F	174.8 \pm 11.8	4.7 \pm 5.3	76.9 \pm 1.5	227.5 \pm 4.7	113.1 \pm 6.5
	134–211 (473)	0–52 (399)	71.9–82.5 (466)	212–242 (455)	92–134 (456)
MF	184.5 \pm 12.4	5.6 \pm 6.6	80.1 \pm 1.4	229.4 \pm 4.3	115.1 \pm 6.8
	146.5–215 (253)	0–48 (231)	75.0–83.4 (250)	220–243 (247)	90–133 (246)
MFF	179.3 \pm 9.8	6.7 \pm 6.0	79.4 \pm 2.1	229.0 \pm 4.3	114.1 \pm 7.8
	162–194.5 (19)	1–24 (16)	76.6–82.3 (19)	222–236 (19)	101–130 (18)
All M	184.2 \pm 12.3	5.7 \pm 6.5	80.1 \pm 1.5	229.3 \pm 4.3	115.0 \pm 6.9
	146.5–215 (272)	0–48 (247)	75.0–83.4 (269)	220–243 (266)	90–133 (264)
All	177.9 \pm 12.9	5.6 \pm 6.4	78.0 \pm 2.1	228.7 \pm 4.6	112.9 \pm 7.2
	134–222 (2,515)	0–59 (2,039)	71.7–83.8 (2,301)	211–243 (2,436)	90–145 (2,430)

Ranges are given below the means, and sample sizes are in parentheses. The sample sizes in the row labeled “All” are larger than the column totals, because this row includes individuals of unknown sex

Table 2 Correlations among traits: Pearson correlation coefficients and sample sizes (in parentheses) are shown for pairs of traits, with females above the diagonal and males below

Trait	Tail length	Head length	Wing	Mass	Laying date	Age	PC1
Tail length		0.22**** (466)	0.22**** (455)	0.14** (456)	-0.25**** (455)	0.41**** (131)	0.29**** (432)
Head length	0.16* (269)		0.23**** (449)	0.29**** (449)	-0.15** (449)	0.12 (129)	0.77**** (432)
Wing	0.25**** (266)	0.26**** (263)		0.13* (438)	-0.16** (438)	0.02 (128)	0.61**** (432)
Mass	0.09 (264)	0.29**** (261)	0.11 (258)		-0.36**** (440)	0.13 (127)	0.68**** (432)
Laying date	-0.25**** (265)	-0.21*** (262)	-0.15† (259)	-0.39**** (257)		-0.61**** (129)	-0.32**** (418)
Age	0.37** (67)	0.04 (66)	0.14 (64)	0.25† (66)	-0.78**** (66)		0.14 (122)
PC1	0.22** (255)	0.79**** (255)	0.59**** (255)	0.69**** (255)	-0.37**** (248)	0.20 (62)	

Laying date is standardized by year and square-root transformed, and age is ln transformed. PC1 is the first principal component of head length, wing length and body mass, with measurements standardized by sex

Significant correlations: **** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.005$, * $p < 0.01$, † $p < 0.05$

FM and FF in body mass and length of the wings and head (Table 1) show that FM were also significantly heavier ($t_{360} = 2.81, p = 0.005, d = 0.30$), but these groups did not differ significantly in head length ($t_{370} = 1.47, p = 0.14, d = 0.15$) or wing length ($t_{360} = 0.03, p = 0.98, d = 0.003$).

Tail length was associated with other variables, and these variables were often associated with each other (Table 2). Most of these correlations were highly significant and would remain significant with correction for multiple comparisons, although most of the correlation coefficients were small to intermediate (Table 2). Except for body mass in males, tail length was positively correlated in both sexes with head length, wing length, body mass, and PC1 (Table 2). Tail length also increased with age (Fig. 1; Table 2) and was higher among terns nesting early in the breeding season (i.e. a significant negative correlation between tail length and laying date; Table 2). Age was not significantly correlated with head length or wing length in either sex, nor with body mass in females. Laying date was strongly negatively correlated with age and was negatively correlated with the body size variables (Table 2).

In the longitudinal analysis (see “Methods”), the regression coefficient b between $(t_{ij} - t_{ik})$ and $(y_j - y_k)$ was significant among young birds ($b = 6.63 \text{ mm year}^{-1}; F_{1,38} = 5.98, p = 0.019, r^2 = 0.14$), but not in older birds ($b = 0.00 \text{ mm year}^{-1}; F_{1,39} = 0.00, p = 1.00, r^2 = 0.001$). The first regression coefficient did not differ significantly from that observed in the cross-sectional analysis (Fig. 1; $b = 1.79 \text{ mm year}^{-1}$ after excluding birds included in the longitudinal analysis; $t = 1.74, p = 0.083$), but the second was significantly different ($t = 2.17, p = 0.030$). Hence, the relationship between tail length and age observed in the cross-sectional analysis (Fig. 1) appears to have reflected growth among birds ≤ 6 years old, but there was no significant evidence for growth among older birds.

To control for covariance among variables and further examine factors associated with tail length, we ran two

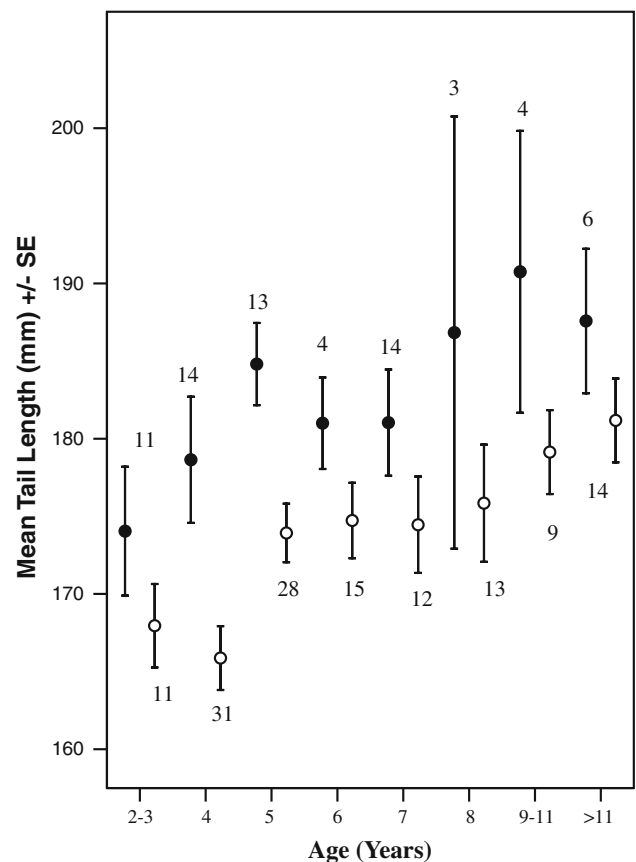


Fig. 1 Mean length (\pm SE) of tail streamers of Roseate Terns (*Sterna dougallii*) across age classes. Closed circles males and open circles females. Numbers above and below the error bars indicate sample size. In an ANCOVA including sex as a variable, the joint slope is 1.98 (SE = 0.37; $F_{2,199} = 26.60; p < 0.0001$)

(cross-sectional) General Linear Models with tail length as the dependent variable. The first GLM included the following variables: sex category (MF, FM, FF), laying date (standardized and transformed as described above), and PC1 (see “Methods”). The second GLM also included age (ln transformed) and was done separately, because

Table 3 General linear models with tail length as the dependent variable

Variable	<i>F</i> value	<i>df</i>	<i>p</i> value	<i>B</i> (SE)	Partial η^2
(a) Model 1 (age excluded): overall $F_{4,566} = 42.95$, $p < 0.0001$, adjusted $r^2 = 0.23$					
Sex category	50.69	2	<0.0001		0.15
PC1	21.67	1	<0.0001	2.35 (0.51)	0.037
Laying date	13.08	1	<0.0001	-1.61 (0.45)	0.023
(b) Model 2 (age included): overall $F_{5,145} = 13.07$, $p < 0.0001$, adjusted $r^2 = 0.29$					
Sex category	11.33	2	<0.0001		0.14
Age	22.40	1	<0.0001	14.11 (2.98)	0.13
PC1	10.89	1	0.001	3.23 (0.98)	0.070
Laying date	3.76	1	0.055	2.07 (1.07)	0.025

The following independent variables are included: sex category (MF, FM, FF), laying date and PC1 (first principal component of head length, wing length and body mass, with measurements standardized by sex). Model 2 also includes age. Parameter estimates (*B*) for continuous variables are given with standard errors in parentheses

including age reduced the sample size from 571 to 151. Both GLMs were highly significant and explained more than 22 % of the variance in tail length (Table 3). In Model 1, all three variables were significantly related to tail length. Of these, sex category was the variable explaining the highest proportion of the variance (partial $\eta^2 = 0.15$; Table 3a), and Bonferroni-adjusted pairwise comparisons showed significant differences among all three sex categories (MF vs. FM, $p < 0.0001$; MF vs. FF, $p < 0.0001$; FM vs. FF, $p = 0.017$). When age was included in Model 2, the effects of both age and sex category were highly significant ($p < 0.0001$) and these two factors explained similar proportions of the variance in tail length (partial $\eta^2 = 0.13$ and 0.14, respectively; Table 3b). Body size (PC1) also made a significant contribution to explaining variation in tail length (Table 3b), but the relationship with laying date was marginal ($p = 0.055$). No significant interaction effects occurred in these models and including interaction effects did not improve the r^2 values.

Tail symmetry

Based on repeated measurements of tail streamers in 2009, significant FA in tail length was present (sides \times individuals $F_{231,468} = 52.04$, $p < 0.0001$) with no significant directional asymmetry (sides $F_{1,468} = 0.97$, $p = 0.327$). There was also no evidence for directional asymmetry when including data from all years (mean right minus left not significantly different from zero: $t_{2038} = 0.72$, $p = 0.47$). The significant sides \times individuals interaction indicates that FA is greater than measurement error (Palmer 1994; Palmer and Strobeck 2003), which comprised only 1.9 % of the between-sides variance.

Male FA was higher than female FA (Table 1; unpaired $t_{444,5} = 2.06$, $p = 0.040$; the non-integer degrees of freedom were because equal variances could not be assumed).

There was no significant relationship between tail length and tail FA, whether comparing across the dataset ($r_s = -0.041$, $n = 2,039$, $p = 0.064$) or if the data were divided by sex (males: $r_s = -0.093$, $n = 247$, $p = 0.15$; females: $r_s = -0.004$, $n = 399$, $p = 0.94$).

Fluctuating asymmetry was significantly but weakly correlated within individuals across years (repeatability $r = 0.097$, $F_{298,306} = 1.23$, $p = 0.036$) and was not significantly correlated with other traits. Pairwise correlations between FA and head length, wing length, body mass, and PC1 were all non-significant (females: all $\text{abs}(r_s) < 0.05$, all $p > 0.34$; males: all $\text{abs}(r_s) < 0.08$, all $p > 0.21$). The only significant correlation was with age in males, and this was opposite to the predicted direction (male age: $r_s = 0.27$, $n = 60$, $p = 0.039$ uncorrected for multiple comparisons; female age: $r_s = 0.14$, $n = 110$, $p = 0.15$).

There was no significant difference in mean tail FA between females mated to males and those mated to females (Table 1; $t_{312} = 0.78$, $p = 0.44$, $d = 0.09$). Despite the significant sex difference in FA (above), comparisons among sex categories were not significant and none of the covariates significantly predicted FA (GLM with age excluded: $F_{4,496} = 2.12$, $p = 0.077$, adjusted $r^2 = 0.009$; with age included: $F_{5,123} = 1.04$, $p = 0.40$, adjusted $r^2 = 0.002$).

Although there was no significant difference in FA between FM and FF, birds with one broken or missing tail streamer were more frequent among FF than among FM. Excluding females with a mate of unknown sex, females in multi-female associations comprised 41.1 % of 314 females with intact tails, but 57.4 % of 68 females with one broken or missing tail streamer ($\chi^2_1 = 5.36$, $p = 0.021$). Similarly, when we examined females with two intact tail streamers at the extreme of the asymmetry distribution (90th percentile for females = 10 mm), 53.1 % of 32 females were mated to females, compared to 39.7 % of 282

females with tail FA <10 mm. However, these distributions did not differ significantly ($\chi^2_1 = 1.62$, $p = 0.20$). Including those with mates of unknown sex, highly asymmetrical females did not lay significantly later than other females ($t_{383} = 0.46$, $p = 0.64$), nor did females with one broken tail streamer ($t_{584} = 0.32$, $p = 0.75$).

Correlations between mates

Among 56 birds encountered with banded mates in two successive years, 22 (39 %) had retained the same mate. Among 194 birds encountered with banded mates in two different years, logistic regression yielded the following equation for $p(n)$, the probability that the focal bird would have the same mate after n years:

$$\text{Logit}(p) = -0.080 + (0.389 \pm 0.116)n$$

(Wald $\chi^2 = 11.11$, $p < 0.001$).

This led to an estimate of 1.73 years for the mean duration of pair-bonds, including the year in which each pair was formed. Multiple logistic regression revealed no significant dependence of p on the age of the focal bird (partial regression coefficient = 0.036 ± 0.116 , $n = 65$, Wald $\chi^2 = 0.10$, $p = 0.75$).

Mates were significantly positively correlated in both tail length (correlation between males and their mates, $r_{193} = 0.27$, $p < 0.0001$) and age ($r_{17} = 0.66$, $p = 0.002$). Because the sample size for known-sex pairs of terns with both mates of known age was small, we also tested for an age correlation among pairs of unknown sex that were presumed to be male–female pairs ($r_{69} = 0.50$, $p < 0.0001$). The correlation among mates in tail length remained significant when controlled for laying date with multiple regression (male tail length as dependent variable, $n = 191$; for female tail length, partial $r = 0.17$, $p = 0.018$; for laying date, partial $r = -0.26$, $p < 0.0001$) and was marginal when controlled for pair age ($n = 79$; for female tail length partial $r = 0.21$, $p = 0.072$; for pair age, partial $r = 0.30$, $p = 0.007$). If the correlation in tail length among mates resulted simply from the correlation in age, then mates that differed more in age should also have differed more in tail length. Although there was a trend in this direction, the positive correlation between age difference and tail length difference was not statistically significant (all presumed male–female pairs: $r_{64} = 0.19$, $p = 0.13$; known-sex pairs only: $r_{17} = 0.05$, $p = 0.83$).

There was also a positive correlation between mates in body size index ($r_{166} = 0.17$, $p = 0.028$), but this correlation was not significant when controlled for laying date (partial $r = 0.069$, $p = 0.34$; for laying date, partial $r = -0.37$, $p < 0.0001$) or pair age (partial $r = 0.063$, $p = 0.59$; for pair age, partial $r = 0.24$, $p = 0.041$). There

was no significant correlation in tail FA between mates ($r_s = -0.040$, $n = 149$, $p = 0.63$).

Discussion

In sexually monomorphic species with biparental care, mutual mate choice may occur (Trivers 1972; Jones and Hunter 1993; Amundsen 2000; Kokko and Johnstone 2002; Kraaijeveld et al. 2007; Rowe and Weatherhead 2011). Both females and males are expected to be choosy when selecting a mate, and we found evidence suggesting the importance of tail length in sexual selection for both sexes. Tail length was correlated between mates, which is consistent with mutual mate choice but could also result from passive processes, such as similarity in the age of mates (see below). Males are larger and have longer tails than females (Gochfeld et al. 1998; Table 1), which implies that Roseate Terns evolved with stronger sexual selection on males. On the other hand, because of the female-biased sex ratio in Roseate Terns of the Northwest Atlantic, males are a limiting resource (Nisbet and Hatch 1999). Many female Roseate Terns have low reproductive success as part of multi-female associations or fail to nest, so sexual selection may be expected to also act strongly on females. We demonstrated that females in female–female pairs or other multi-female associations had shorter tails than those paired to males, consistent with male choice based on female tail length or characters correlated with it.

We found that mates are correlated in age as well as in tail length. It could be hypothesized that the correlation in age results from birds forming pairs early in their breeding careers and then retaining the same mates as they grow older (Ludwig and Becker 2008). However, the mean duration of pair bonds was only 1.73 years at this colony and less than 2.5 years at another colony (Nisbet et al. 1998). Hence, older birds must also select mates of similar ages. Because tail length increased with age in birds up to age 6 years, it may be that tail streamers serve in part as an indicator of age (Manning 1985; Regosin and Pruett-Jones 2001). Among older birds, however, tail length increased with age in the cross-sectional analysis (Fig. 1), but there was no significant evidence for growth in the longitudinal analysis (see “Results”). This suggests that birds with longer tails survived better into the older age classes, another manifestation of the relationship between tail length and individual quality.

It could also be hypothesized that the correlation between mates in tail length might result from birds selecting mates according to age. Multiple regression analysis showed that tail length in males was correlated with both female tail length and with pair age, and the correlation between age difference and tail length

difference was not significant. However, our sample of known-age, known-sex pairs was small, and the relationship with female tail length was only marginally significant ($p = 0.072$) after controlling for pair age. Hence, we cannot fully reject this hypothesis. However, if birds use tail length as one of the cues by which they assess the age of potential partners, as suggested in the previous paragraph, the distinction between selecting mates by age and by tail length would not be meaningful.

An important correlate of reproductive success in terns, laying date (Burger et al. 1996; Arnold et al. 2004), varied with both tail length and age. There are also advantages to pairing with an experienced mate (Ludwig and Becker 2008). By choosing a mate with a longer tail, a tern may gain both a more experienced mate and a mate with higher phenotypic quality. Because the increase in tail length with age appeared to switch from growth to selection, there was support for both the “constraint” and “selection” hypotheses for improvements in reproductive success with age (see Limmer and Becker 2007), but their relative importance may change from constraint among young adults to selection among older adults. Body mass, another correlate of reproductive success in terns (Wendeln 1997; Wendeln and Becker 1999; Limmer and Becker 2007), was also positively correlated with tail length and age, but body mass measured more than 2 weeks after laying may not reflect mass at the time of pairing (Choudhury et al. 1992; Ludwig and Becker 2008). Ludwig and Becker (2008) suggest that, in Common Terns, female body mass during incubation likely reflects male quality, due to courtship feeding.

One might expect that males in multi-female associations would be high-quality males that have attracted more than one mate. Unfortunately, we have few data on such males, because most multi-female associations included no males (Nisbet and Hatch 1999). However, the available data suggest that these males were of low quality, based on tail length, body size and perhaps FA (see Table 1). They also began nesting later than males mated monogamously to females, with a median laying date 3.5 days later (approximately the 76th percentile). Behavioral observations at another northwest Atlantic colony suggest that trios develop when a low-quality female mated to a male is unable to prevent another female from joining the pair (J. Spindel, personal communication), perhaps an example of intrasexual selection in females (Rosvall 2011). Males paired with low-quality females are therefore likely to be themselves of low quality, particularly in a population with an excess of females where males generally can expect to obtain mates of higher quality.

We also examined whether tail symmetry may play a role in sexual selection. Females in multi-female associations did not significantly differ in FA from those mated to males, and FA was not significantly correlated among

mates. We also failed to find evidence supporting the role of tail FA as an indicator trait, because it was weakly correlated within individuals across years, was not significantly correlated with other indicators of quality, and the predicted negative relationship between tail length and tail FA (Møller and Höglund 1991) was absent or at best very weak. However, the correlation between FA in a single trait and an individual's developmental stability is expected to be quite low and therefore difficult to detect (Gangestad and Thornhill 1999; see also Palmer 1994; Palmer and Strobeck 2003).

Terns with one broken tail streamer were overrepresented among females in multi-female associations. (A similar, nonsignificant trend was found for females with extremely high FA.) It may be that females with highly asymmetrical tails were less likely to find male mates, but two observations suggest that the damage to their tail streamers occurred after mate choice: (1) laying dates did not differ significantly from females with two intact tail feathers; and (2) the confined quarters of Roseate Tern nest sites (under vegetation or in nest boxes) provide opportunities for tail streamers to snag and hence to be damaged. This may be especially true for multi-female associations of more than two individuals in which nest reliefs are competitive, rather than orderly and brief. Because tail streamers are susceptible to damage, tail streamer symmetry may not be a reliable indicator of quality (Palmer and Strobeck 2003), although it is possible that high quality individuals are better able to avoid feather damage. True FA is subtle and results from an inability of individuals to develop both sides equally, rather than from damage to feathers (González-Jaramillo and de la Cueva 2010).

In summary, we found correlational evidence supporting the role of tail length in sexual selection, but the best evidence would be an effect of experimental manipulation of tail length on mate choice or parental investment (e.g., Andersson 1982; Møller 1988; Cuervo et al. 1996, 2003). However, the status of the Roseate Tern as an endangered species in the USA (US FWS 1987) precludes such experiments. Experimental studies of mate choice in Roseate or other terns would also be impractical due to the difficulty of trapping the birds prior to pair bond formation, although differential parental investment could still be examined after pair bond formation. The approach used in the current study is likely to be the best alternative to an experimental approach: analysis of a large dataset that is part of a long-term study. Comparative studies may help to explain the range of fork-depths in the tails of terns. It is likely that tail length plays a more important role in sexual selection for Roseate Terns than for other terns, because the tails of Roseates are unusually long relative to wing length, which suggests that other species of terns may rely more on other traits when choosing mates.

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Conflict of interest The authors declare that they have no conflict of interest.

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