NATURAL TAIL STREAMER ASYMMETRY IN MALE MAGNIFICENT FRIGATEBIRDS *FREGATA MAGNIFICENS*: INFLUENCE ON MATE SELECTION AND MALE PARENTAL CARE PERFORMANCE

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Received 16 October 2009, accepted 14 May 2010

SUMMARY

GONZÁLEZ-JARAMILLO, M. & DE LA CUEVA, H. 2010. Natural tail streamer asymmetry in male Magnificent Frigatebirds *Fregata magnificens*: influence on mate selection and male parental care performance. *Marine Ornithology* 38: 85–90.

During the breeding season, birds may have asymmetric tail feathers due to any of the following natural causes: asynchronous growth or molt, wear and tear, breakage or fluctuating asymmetry. Male tail streamer symmetry may be viewed by females as an indicator of male fitness or flight capability, and asymmetry may have a fitness cost in mate selection or parental care performance or both. Here, we explored the possible association between male tail streamer asymmetry, mate selection and male parental care performance in a highly aerial seabird, the Magnificent Frigatebird *Fregata magnificen*s. Our results suggest that natural tail streamer asymmetry of males has neither a fitness cost in mate selection, as there was no correlation between male streamer asymmetry and mating date during the breeding season, nor between male streamer asymmetry and parental care performance. Incubation rate, incubation spell lengths, chick provisioning, chick growth and nest site attendance rates were not significantly correlated with male natural tail streamer asymmetry. Nevertheless, a cost of tail asymmetry may be paid over a longer time period.

Key words: asymmetry, Magnificent Frigatebird, parental care, male quality, sexual selection

INTRODUCTION

Bird tail streamer asymmetry may result from asynchronous growth or molt, wear and tear, breakage or fluctuating asymmetry (random departures from bilateral symmetry that appear when an individual is unable to develop equally on both sides of the body; Møller & Höglund 1991, Bjorksten *et al.* 2000). Here, we refer to "natural asymmetry" as differences in length of bird tail streamers due to any of the causes named above. Tail streamer asymmetry considerably reduces lift force and maneuverability in birds (Evans & Thomas 1992, Balmford *et al.* 1993, Thomas 1993a, b, Evans 1998, Rowe *et al.* 2001); aerodynamic costs must be compensated for if the bird is to compete successfully with more symmetric individuals. Tail streamer symmetry has been shown to be viewed by conspecifics of both sexes as an indicator of male quality during mate choice or male–male competition (Møller & Höglund 1991, Evans 1993, Andersson 1994, Nilsson 1994). Several studies, mainly in the Barn Swallow *Hirundo rustica,* have assessed the role of tail streamers on mate selection and fitness (Møller 1990a, b, 1991, 1992, Møller *et al.* 1998, Hedenström 1995, Hedenström & Møller 1999) and on aerodynamic performance (Balmford & Thomas 1992, Norberg 1994, Evans 1998, 1999). Although a large effort has been directed at assessing effects of secondary sexual characteristics on paternity, mate selection and breeding performance by manipulating tail symmetry and length (Møller *et al.* 1998), the possible effects of natural tail streamer asymmetry have been little studied.

Parental care is costly, especially when one sex invests less through desertion (Osorno & Székely 2004). It is related to the rate at which the young must be fed, and these provisioning rates, along with other maintenance costs, vary with chick growth rates (Furness & Monaghan 1987). Biparental care results in conflict between the male and the female over the division of labor, as each member of the pair would prefer that its mate do most of the work (Jones *et al.* 2002). Dissimilar roles may be determined by different selection pressures acting on males and females that differ in size (Fraser *et al.* 2002).

The Magnificent Frigatebird *Fregata magnificens* (hereafter, frigatebird) is a reverse sexual size-dimorphic, sequentially monogamous (Diamond 1972, 1973), highly aerial tropical seabird (Weimerskirch *et al.* 2003, 2006), characterized by a long and deeply forked tail. Mate choice involves females choosing among males in full display (Madsen *et al.* 2004, 2007a, b), including a fully spread tail. Once a pair forms and copulates, one egg is laid, which is always guarded by one adult (Osorno 1996). Frigatebirds have a long period (12 to 18 months) of parental care of a single altricial chick (Nelson 1975, Osorno 1996): three months of biparental care, followed by male desertion, while the female continues feeding the chick even after it fledges (Diamond 1972, 1973, Osorno 1999, Osorno & Székely 2004). Thus, there is a remarkable division of labor between sexes.

Our goal was to assess whether the natural tail streamer asymmetry of male frigatebirds influences mate selection and male parental care performance during the breeding season. The following predictions were investigated on the basis of the hypothesis that natural tail streamer asymmetry of males has fitness or aerodynamic costs that would affect mate selection or male parental care performance or both. If natural tail streamer asymmetry of males influences mate selection, we expected a positive correlation between tail streamer asymmetry and later pair formation date. If natural tail streamer asymmetry of males influences male parental care performance, we expected significant negative correlations between male tail streamer asymmetry and male incubation rate, incubation spell length, chick provisioning, chick growth and nest-site attendance rates.

METHODS

Study area

We conducted this study during the 2000–2001 breeding season at Isla Isabel National Park off the Central Mexican Pacific coast (21°52′N, 105°54′W), home to one of the largest breeding colonies of frigatebirds in Mexico (15 000–16 000 birds; Madsen *et al.* 2007a).

Data collection

We caught breeding adult mates once by hand at night (n = 26 males, n = 24 females; 2 females could not be captured) and removed them from their nests and from the colony. Frigatebirds were marked by placing yellow canvas wing tags with black numbering (20.5 × 8 cm and 10.8 g; approximately 1% of the mass of the lightest individuals) on the left wing and a numbered metal ring on the left leg. Length of tail streamer was measured (±0.5 mm) by the same person at least twice, and we recorded the result once we obtained identical measurements.

We conducted focal observations of breeding pairs (n = 26) from incubation (n = 21) or rearing of a chick from 1–10 days old (n = 5) until the chick died (n = 5) or reached 30 days of age (n = 21). The 26 focal nests were observed simultaneously for three hours daily during the peak activity period in the colony, i.e., when most chicks were being provisioned. We determined peak activity to fall between 11h00 and 14h00 by observing the colony during three consecutive days from 07h00 to 19h00. We observed breeding pairs from a site located 15–75 m from the nests and recorded the following behaviors: (a) presence and sex of adult on nest, (b) arrivals of adults to the nests and departures of adults from the nests and (c) chick provisioning frequency and sex of the parent feeding the chick. We made a scan for the presence of parents and chicks on the nest every 30 min. During weekly nocturnal visits to the nests, we measured culmen and ulna lengths of chicks (n = 26) using a measuring tape (±0.5 mm) and mass using a Pesola spring balance (±25 g).

Data analysis

To analyze tail streamer asymmetry of breeding pairs, we calculated (1) the absolute degree of asymmetry as the numerical difference between right and left outer tail feather and (2) the relative degree of asymmetry as measure [1] divided by the average size of the trait (Palmer & Strobeck 1986, Møller & Höglund 1991). We assigned pair formation date based on the hatching date of the chick and known lengths of reproductive stages: three weeks for courtship display and copulation, and four weeks for incubation (Diamond 1972, 1973, Osorno 1996). We calculated male parental investment as (a) incubation rate (male total time spent sitting on the egg divided by the total observation time), (b) mean length of incubation spells (male incubation time [days] before relief divided

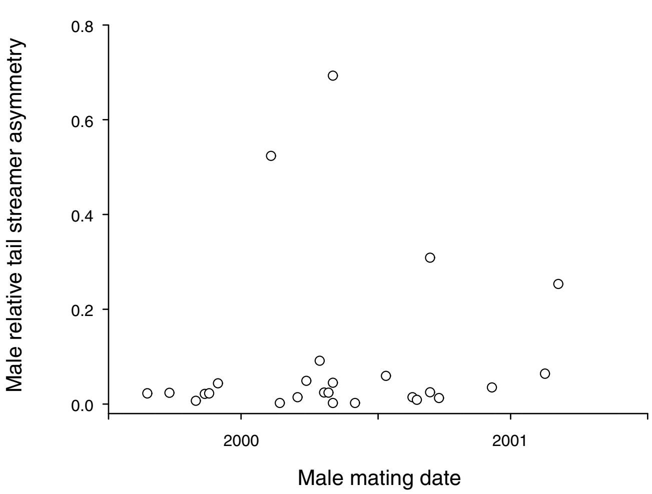
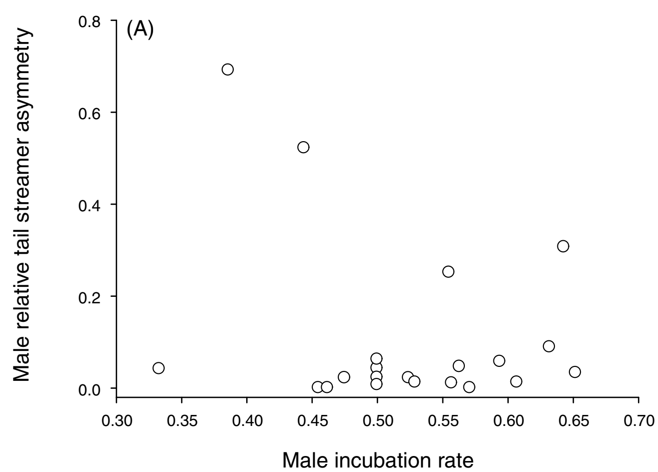


Fig. 1. Magnificent Frigatebird *Fregata magnificens* male relative tail streamer asymmetry and male mating date during the breeding season (2000–2001), Isla Isabel, México.



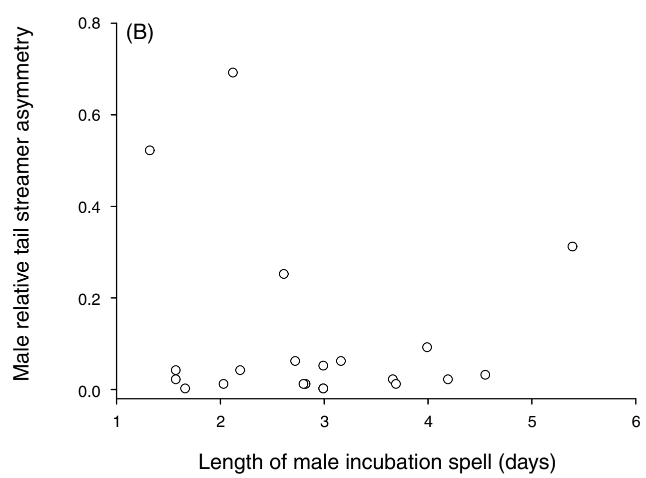


Fig. 2. Male relative tail streamer asymmetry in relation to (a) male incubation rate (male total time spent sitting on the egg/total observation time), and (b) mean length of incubation spell (days) of Magnificent Frigatebirds *Fregata magnificens,* breeding season 2000–2001, Isla Isabel, México.

by the total spells), (c) chick provisioning rate (number of times the male parent fed the chick divided by total feeds [exploring also whether a low chick provisioning rate of a male was compensated by its mate]), (d) chick growth rate (cm/day), estimated by fitting a von Bertalanffy curve (with data on culmen length from five chicks of known age used to estimate initial ages of the chicks; Osorno & Székely 2004, Tobón & Osorno 2006) and (e) nest-site attendance (male time on nest while not incubating [i.e., brooding only] divided by total observation time).

We used one-way analysis of variance (ANOVA), with individual as the factor, to assess repeatability of male behavioral measures (i.e., length of incubation spells, chick provisioning and nest-site attendance). Pearson's correlation coefficient was used to measure the association between male tail streamer asymmetry and pair formation date, female and male provisioning rates, and other male behaviors. To test whether tail length (as distinguished from asymmetry per se) was used by females as a possible indicator of male quality, we also computed Pearson correlation coefficients between male parental care performance and tail length. Sample sizes varied among correlation tests according to available data: male relative tail streamer asymmetry and mating date, chick provisioning, chick growth and nest site attendance (n = 26); male and female provisioning rate (n = 24); male relative tail streamer asymmetry and incubation rate, as well as length of incubation spells (n = 20). All conclusions assumed a significance level of $P = 0.05$ (Zar 1999). We report mean ± SD.

RESULTS

ANOVA of behavior variables of males were highly significant: length of incubation spells ($F_{1,19} = 1.989$, $P = 0.016$), chick provisioning ($F_{1,25} = 1.687$, $P = 0.019$) and nest site attendance ($F_{1,25} = 3.383$, $P = 0.016$). Nevertheless, we found no significant correlation between male relative tail streamer asymmetry and male mating date (n = 26, $r = 0.109$, $P = 0.594$; Fig. 1), male incubation rate (0.523 ± 0.082; n = 21, $r = –0.267$, $P = 0.240$; Fig. 2a), or the length of incubation spells (n = 21, $r = –0.148$, $P = 0.501$; Fig. 2b). Males accounted for 52% of observed incubation time, and their median length of incubation spells was 2.92 ± 1.06 days, range 0.5 to 10 days.

Although males accounted for only 38% of the observed feedings, low provisioning rates of males were not compensated by their mates. Instead, we found a significant positive correlation between male and female provisioning rates within pairs (n = 24, $r = 0.720$, $P < 0.001$; Fig. 3a). We did not find a significant correlation between male relative tail streamer asymmetry and male chick provisioning

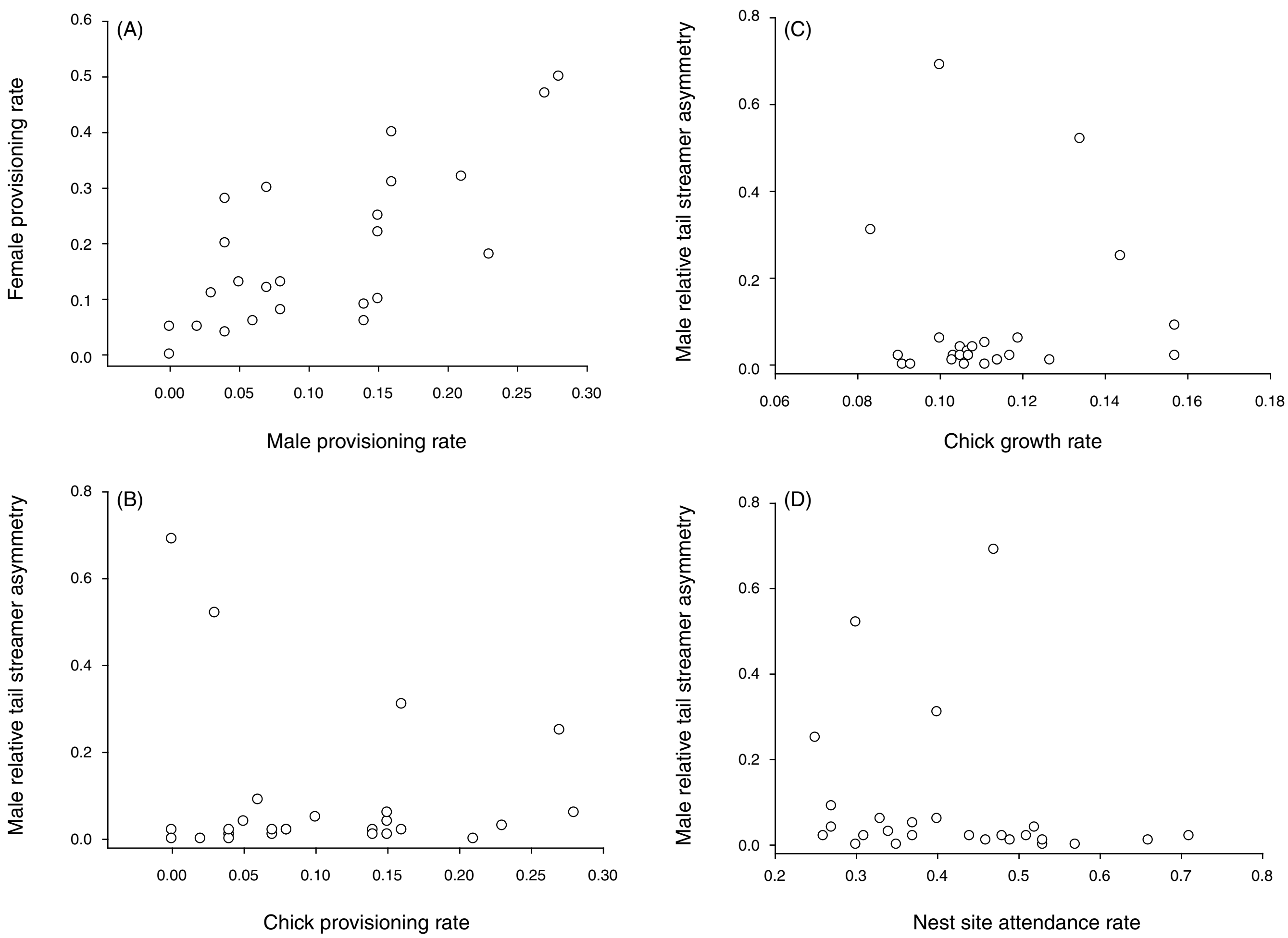


Fig. 3. Correlation of chick provisioning rates (number of parent feeds/number of total feeds) of males and females (a), and male tail streamer asymmetry in relation to (b) chick provisioning rate of males, (c) chick growth rate (cm/day) and (d) nest-site attendance rate (male brooding time on nest/total observation time) in Magnificent Frigatebirds *Fregata magnificens,* breeding season 2000–2001, Isla Isabel, México.

rate (0.105 ± 0.082; n = 26, r = –0.125, P = 0.549; Fig. 3b), or between male relative tail streamer asymmetry and chick growth rate (0.112 ± 0.019; n = 26, r = 0.068, P = 0.743; Fig. 3c). There was no significant correlation between male relative tail streamer asymmetry and male nest-site attendance (0.419 ± 0.124; n = 26, r = –0.177, P = 0.386; Fig. 3d). Males attended the nest 41% of the time (females attended 37% of the time; with chicks left alone 22% of the time).

There was no significant correlation between male tail length and mating date (n = 26, r = –0.252, P = 0.215, Fig. 1), nor between male tail length and male parental care performance: male incubation rate (n = 20, r = 0.189, P = 0.414), length of incubation spell (n = 20, r = 0.125, P = 0.589), chick provisioning (n = 26, r = 0.003, P = 0.987), or nest-site attendance (n = 26, r = –0.109, P = 0.595).

DISCUSSION

Our results suggest that natural tail streamer asymmetry of male frigatebirds carried no fitness costs in mate selection. Tail-symmetric males did not obtain a mate earlier in the breeding season, and we found no evidence that male natural tail streamer asymmetry affected male parental care performance. Because incubation rate, length of incubation spells, chick provisioning, chick growth and nest-site attendance rates showed no significant correlations with male natural tail streamer asymmetry or tail length, there was no detectable advantage to females in choosing a tail streamer-symmetric male, or one with a longer tail.

Male relative tail streamer asymmetry and mate selection

Sexually selected traits usually predict mate selection patterns and correlate positively with measures of seasonal reproductive success (Andersson 1994), but male frigatebirds with more symmetric and longer tails mated and bred as successfully as those with more asymmetric and shorter tails. Low correlation between male relative tail streamer asymmetry and male mating date suggests other factors constitute the primary influence on female choice. Although natural selection may favor males whose outer tail feathers are close to an aerodynamic optimum (Buchanan & Evans 2000, Evans 1998), and the extent of tail streamer asymmetry, as well as tail length, could be used as an honest signal of male quality (Møller 1990a, b, 1991, 1992, Møller & Höglund 1991, Møller *et al.* 1998), such characteristics are not the only ones that a female frigatebird might assess when choosing a mate. Females could discriminate among males on the basis of general body characteristics, providing a better estimate of general condition (Balmford & Thomas 1992, Møller & Pomiankowski 1993, Goddard & Lawes 2000, Safran & McGraw 2004). In addition to tail streamer and length, frigatebirds exhibit ornamental traits including bright iridescent plumage and a red inflatable gular pouch that produces a drumming display during courtship (Madsen *et al.* 2004, 2007a, b). Among those characteristics, only low-frequency drumming (correlated with the size of the gular pouch and the age of the frigatebird) significantly predicted male mating success, likely because drumming reflected male stamina (Madsen *et al.* 2007a). In North American Barn Swallows, plumage coloration—not tail streamer asymmetry, as reported for European Barn Swallows—best predicted patterns of pairing and seasonal reproductive success (Safran & McGraw 2004). Similar to findings for North American Barn Swallows, we found tail streamer asymmetry did not prove to have an important role in frigatebird mate selection.

Male relative tail streamer asymmetry and male parental care performance

Although pelecaniforms do not develop an incubation patch (Whittow 2002), and incubation in a warm climate probably requires little or no excess heat production, a prolonged incubation period may indicate energy limitation (Ricklefs 1983). Male frigatebirds had a higher incubation rate than females and, contrary to an earlier finding in this species (Osorno 1996) and in the Great Frigatebird (*Fregata minor*; Dearborn 2001), male frigatebirds had long incubation spells on average. However, neither male incubation rate nor length of incubation spell increased with decreasing tail streamer asymmetry. Symmetric and asymmetric adult male frigatebirds may have similar energy reserves during incubation, but this hypothesis must be addressed in the future.

Low chick provisioning rates of males were not compensated by their mates, suggesting a female with an underperforming mate incurred no added energy costs during chick provisioning. It has been suggested that in long-lived and sequentially monogamous species like the Magnificent Frigatebird, some degree of "retaliation" might be expected when females are faced with low parental effort by their mates (Dearborn 2001). Although male frigatebirds feed the chick less often than females during biparental care, full compensation by females occurs only after male deserts (Osorno and Székely 2004). Male tail streamer asymmetry probably adds flight costs but was uncorrelated with chick provisioning or chick growth rate. Because brooding males spent more time attending the nest than females, the energy expenditure of males probably was little affected by tail asymmetry during chick rearing.

To summarize, neither tail streamer asymmetry nor tail length of male frigatebirds had measureable fitness costs in this study. We found no evidence that longer-tailed males were preferred by females, and the absence of correlations between male tail length and male parental care performance suggests that tail length was not useful to females as a quality indicator. Nevertheless, subtle costs of asymmetry may be paid over a longer time period, with asymmetric males having lower lifetime breeding success than symmetric ones. Future work on energetic costs of tail streamer asymmetry over an extended period, in contrast to the short-term effects we investigated, is needed to answer conclusively the question of fitness costs of tail streamer asymmetry in the Magnificent Frigatebird.

ACKNOWLEDGEMENTS

José Luis Osorno provided indispensible guidance on research design. Vinni Madsen, Robert Mesta and Robert Elner critically reviewed the draft manuscript. We thank Emilio Tobón for his advice on chick measurements and data analysis, and Juan Carlos Pérez and Christian Schlögl for help with the field work. The Comisión Nacional de Áreas Naturales Protegidas (CONANP) and the Mexican Navy provided logistical support. The Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) issued our permit to work at Isla Isabel. Fishermen of San Blas and Boca de Camichin helped us in innumerable ways. We appreciate valuable suggestions by an anonymous reviewer.

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