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Courtship display by great frigatebirds, *Fregata minor*: an energetically costly handicap signal?

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Abstract We used detailed time-budget observations, mark-resight data, and doubly labeled water estimates of energy expenditure to test whether energy spent on courtship display by male frigatebirds functions as a sexually selected handicap signal. During a 2-day period of time budget observations, males displayed on average 29.5% of the time (range 0–100% for 15 different males), and this value was correlated with an index of season-long display effort. Season-long display effort was strongly predictive of pairing success. Average field metabolic rate (FMR) during the 2-day time budget period was 676.5 kJ/day (range 464.8–1035.0), substantially lower than the mass-specific FMR predicted from studies of other seabirds during incubation or chick-rearing. Despite a low overall FMR, display effort could function as an energetic handicap, either if FMR correlates positively with the amount of courtship performed or if high-quality males display at a high rate because they pay a lower energy cost per unit of display than do low-quality males. We found no relationship between FMR and display rate, despite good power for doing so. We also did not find a significant difference in energy spent divided by courtship time for males that were or were not chosen by females (inferred to be high- and low-quality males, respectively), though the medians differed in the

predicted direction (preferred males having lower relative costs than non-preferred males) and the confidence interval on the difference between groups was very wide. Thus, we found evidence that male courtship effort is predictive of pairing success, we rejected one mechanism by which energetic cost of display could function as a handicap, and our test of the alternate energetic handicap mechanism was equivocal.

Keywords Doubly labeled water · Field metabolic rate · Handicap · Mate choice · Seabird

Introduction

Many animal signals, such as courtship displays of males to females (Kodric-Brown and Brown 1984; Andersson 1994) or begging behaviors of offspring to parents (Johnstone and Godfray 2002), are useful to the receiver only if they convey information about the individual producing the signal. Most theoretical treatment of signal evolution has suggested that these sorts of signals must be constrained, typically by cost, in order to remain informative (Grafen 1990; Godfray and Parker 1992; Maynard Smith and Harper 2003), and handicap theory has proposed that particular signals are used in these contexts precisely because of their intrinsic costs (Zahavi 1975, 1977).

Part of the rationale behind the evolutionary requisite for cost is the recognition that these situations frequently entail at least some degree of conflict of interest between the signaller and the receiver. This conflict is seen clearly both in the example of parent-offspring communication regarding offspring need (Trivers 1974; Wright and Leonard 2002) and in mate choice (Hill 1994; Watson et al. 1998). However, the evidence for the cost of such signals is mixed. For example, some studies have found a growth cost to begging by nestling birds, implying an energetic cost (Kilner 2001; Rodriguez-Girones et al. 2001), whereas other studies have found little impact of begging on overall energy expenditure (Leech and Leonard 1996; McCarty 1996; Bachman and

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Chappell 1998) or on growth (Kedar et al. 2000; Leonard et al. 2003); the evidence is likewise weak with regard to a predation cost of begging (reviewed in Haskell 2002). In terms of mate choice, several studies of anurans have found very elevated metabolic rates during bouts of calling (Bucher et al. 1982; Prestwich et al. 1989; Wells and Taigen 1989), and there are also striking examples of predation costs of courtship calls by frogs (Tuttle and Ryan 1981). However, the evidence from other taxa is less clear. In birds, the metabolic cost of song was shown to be high in Carolina wrens *Thryothorus ludovicianus* (Eberhardt 1994; but see Gaunt et al. 1996) but not in roosters *Gallus gallus* (Chappell et al. 1995; Horn et al. 1995), pied flycatchers *Ficedula hypoleuca* (Ward et al. 2004), zebra finches *Taeniopygia guttata* (Franz and Oberweger 2003), or canaries *Serinus canaria* (Ward et al. 2003). For species with more complex courtship displays, field metabolic rate (FMR) has been found to be related to display rate in sage grouse, *Centrocercus urophasianus* (Vehrenamp et al. 1989), and great snipe, *Gallinago media* (Högland et al. 1992). A further complication with empirical measures of signal cost is that handicap models of signal cost require not that costs be universally high, but rather that different individuals pay different costs for producing a given level of signal (Pomiankowski 1987; Grafen 1990; Maynard Smith and Harper 2003). Thus, meaningful tests for handicapping costs require measurements of signal cost for signalers that differ in state or quality.

Courtship display in great frigatebirds, *Fregata minor*, has the potential to function as a handicap signal. Great frigatebirds are sexually dimorphic seabirds that breed colonially on oceanic islands where they have no predators. Males perform elaborate courtship displays to females (Nelson 1975): they inflate a bright red gular pouch, erect a ruff of iridescent feathers around the neck, tilt and wag the head, extend and shake the wings, and make a loud vocal trill. Males vary in the amount of time spent displaying to prospective mates, and the mate choice arena is characterized by a very male-biased operational sex ratio (Dearborn et al. 2001). As predicted by these circumstances, males have much lower and more variable pairing success than females (Dearborn and Anders, unpublished data), indicating strong sexual selection on males. Though this courtship might thus seem to be a classic example of a sexually-selected handicap signal, no data exist on whether variation among males in courtship display time is linked to variation in mating success or whether courtship display is costly as envisioned by handicap models. Furthermore, field metabolic rate has never been measured during courtship in any seabird.

In this study, we used behavioral observations to test whether variation in male courtship time was predictive of male pairing success, and we used measures of field metabolic rate to test whether courtship display effort has energetic cost patterns that are consistent with handicap theory. Specifically, handicap theory predicts that low-quality males would pay a greater cost for a given level of display (Zahavi 1977; Grafen 1990), manifest here in one of two ways. First, FMR might correlate directly with display

rate across males, as shown in sage grouse (Vehrenamp et al. 1989). In that study, male grouse differed in their foraging ability and hence in their ability to recoup the energy expended in display. Low quality males opted not to display at a high rate because the cost of the increased energy expenditure would be greater for them, due to their lower foraging ability, than it is for high quality males (Vehrenamp et al. 1989). This is the most commonly envisioned mechanism for energetics-based handicaps. Alternatively, though, low-quality males might directly pay a higher energy cost per unit of display time than do high-quality males (e.g., due to lower physiological quality). In that case, no relationship is expected between general FMR and display time, but the ratio of the two (i.e., energy spent per proportion of time spent on display) should be greater for low-quality males than for high-quality males.

Methods

Study population and individual marking

Frigatebirds have a lek-like process of mate choice, featuring male sexual ornaments, female mate choice in a dense aggregation of displaying males, and pair bonds that last for only a single breeding attempt (Dearborn et al. 2001; Dearborn and Ryan 2002). However, frigatebirds are unlike true lekking species in that males contribute extensively to parental care (Nelson 1975; Dearborn 2001).

We studied a population of great frigatebirds on Tern Island, a 14-ha island in French Frigate Shoals, an atoll in the Northwestern Hawaiian Islands ($23^{\circ} 45' N$, $166^{\circ} 17' W$). Frigatebird pair formation and nest initiation occur from January to May. During this time, male frigatebirds perch in bushes to perform courtship displays while females fly over the breeding colony in the initial stages of choosing a mate (Nelson 1975). The operational sex ratio in our study population is male-biased (typically 5 or 6 displaying males per mate-evaluating female), such that females appear to have a wide range of choices for mates (Dearborn et al. 2001), and only 19% of displaying males succeed in attracting a mate in a given breeding season (Dearborn and Anders, unpublished data). Because adult frigatebirds have no predators at the breeding colony, there is no predation risk to limit time spent on courtship display. Foraging by adult males in our population is entirely pelagic, with foraging trips of breeding birds typically lasting 1–8 days (Dearborn 2001).

Field work was conducted from January to May 1999, with initial captures of 17 sexually mature males being made between 3 and 21 February. Birds were captured by hand at night while they were sleeping in bushes in the breeding colony. Captured individuals were weighed and measured, marked with leg bands and vinyl wrap-around wing tags (Dearborn et al. 2003), and equipped with a radio transmitter. The transmitter (Advanced Telemetry Systems, Isanti, Minn.) was attached to a cluster of contour feathers in the center of the bird's back with epoxy resin

(Titan, Lynnwood, Wash.); the total package had a mass of approximately 6 g, which constituted, on average, 0.44% of the bird's body mass.

Field metabolic rate

Measurements of field metabolic rate were obtained using the doubly labeled water (DLW) technique in which the loss rates of ^2H and ^{18}O yield an estimate of CO_2 production and, consequently, of energy expenditure (Lifson and McClintock 1966; Nagy 1980; Speakman 1997). We injected birds intraperitoneally with 6.00 ml of a 1:2 mixture of water containing 99.9 atom% ^2H and 10 atom% ^{18}O using a Hamilton syringe and a 23-ga needle. The injection volume equaled 4.3 μl per gram mass. We weighed birds with a Pesola spring balance that had been calibrated against a Mettler analytical balance. After injection, the bird was housed for 1 h in a small container within which it could sit comfortably. After this 1 h equilibration period (Williams and Nagy 1984; Speakman 1997), a 80–100 μl sample of blood (initial) was removed from the iliac vein, and birds were banded, radio-tagged, and released. Initial levels of ^{18}O averaged 2,921.8 ppm. After 48 h (range: 48:00–48:02) we recaptured birds, took a second blood sample (final), removed the radio transmitter, measured body mass and released the bird. We obtained pre-injection blood samples from three individuals to determine background levels of isotopes. All blood samples were drawn in 15- μl aliquots in un-heparinized microcapillary tubes, flame-sealed, and stored at 4°C until analysis.

Every second night, two new birds were captured and injected and two previously injected birds were sampled for the final time, such that during a given day there were two birds for which we collected time budget data (as described below).

Isotope ratios of $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ were determined in duplicate (initial) or triplicate (final) for each sample at the Center for Isotope Research, University of Groningen (<http://www.cio.phys.rug.nl>; Visser and Schekkerman 1999). The coefficient of variation of the duplicate or triplicate measurements was generally less than 0.02. We calculated CO_2 production using Speakman's equation 7.17 which assumes an evaporative water loss of 25% and a fractionation factor of 0.941 (Speakman 1997). Estimated from isotope dilution, total body water averaged 0.574 ± 0.04 . Validation studies that have compared CO_2 production, as measured gravimetrically, with predictions from the doubly labeled water method have found an average error of 8–10% (Williams and Nagy 1984; Speakman 1997).

CO_2 production can be converted to energy expenditure when the composition of the diet is known (Gessaman and Nagy 1988; Weathers and Sullivan 1989). We assumed that birds were fasting during measurements and hence had an RQ of 0.71; the assumption of fasting was borne out by time budget observations and by radio telemetry data showing that the birds did not leave the island during the 48-h period. We calculated a conversion factor of $27.7 \text{ kJ l}^{-1} \text{ CO}_2$

based on standard conversion factors for fat metabolism (Gessaman and Nagy 1988).

Time budgets

On each of the two mornings between the initial and final blood sample, the bird was located on the island using a radio receiver and a hand-held 3-element Yagi antenna. Continuous behavioral observations were made from approximately 0800 to 1100 hours and 1315 to 1700 hours on both days. Frigatebirds are generally not active at night in this breeding colony, and our analyses assume that differences between males in proportion of time spent on courtship display during the time budget observations would persist during unsampled time periods. Behavioral categories that we recorded included the following components of courtship: gular pouch inflation (four levels: deflated but extended, partly inflated in a small hemisphere, partly inflated in a sphere, and fully inflated), head tilt (i.e., tilted back in display to over-flying females), head wag, vocalization, wings extended in courtship, wing tremble, and erection of the iridescent nape. Non-courtship behaviors were also recorded, including preen, sleep, heat-related postures (including hanging the head in the shade below the body, and rotating the wings upward with the axillary feathers raised; Mahoney et al. 1985), five different aggressive behaviors directed at other males (vocalizations, horizontal head wag, nape erection, snap/bite, and grapple), fly, and out of sight. The head wagging and nape erection that are used in aggressive interactions may be co-opted from courtship displays, though the vocalizations used in aggression are very different from those used in courtship. Some behavioral categories were mutually exclusive (e.g., sleep versus preen) whereas others were not (e.g., erect ruff feathers and vocalize).

Using a stopwatch, we recorded the start and stop times of each type of behavior. The large size of the birds and the open, treeless nature of the island make it easy to conduct these continuous observations. Most birds remained perched nearly the entire time, which allowed detailed categorization of behavior. When birds did fly, they were followed visually until they landed again. With the exception of the start of the observation sessions, telemetry was needed only rarely to relocate birds. For analysis, time spent out of sight was pooled with time spent flying, as birds disappeared from sight only while flying from one part of the island to another; total time flying summed across the 15 males used in analyses was 4 h 11 min 13 s (during 205 h 38 min observation time), and total time out of sight was 0 h 19 min 42 s.

Each bird was observed by a single observer at a time, but the two observers (D.C.D., A.D.A.) switched birds on the second day of time budget observations such that each bird was observed for equal amounts of time by each of the two observers. Order of observer was determined randomly. Concurrent weather data were later downloaded from an automated National Oceanic and Atmospheric Administration weather station located on Tern Island.

Subsequent colony attendance and breeding status

Over the pair-formation and egg-laying part of the breeding season (late January to early May), we surveyed the colony twice per day for the presence of wing-tagged frigatebirds. Surveys, analogous to scan samples of the entire colony, were conducted daily from 20 Jan–2 May 1999 at 1130 and 1700 hours by walking a regular route around the breeding colony such that our search path was never more than 50 m from the birds that we were counting (Dearborn et al. 2003). Frigatebirds are large animals (2 m wingspan) that perch on the tops of low bushes (generally 1 to 2 m high), and Tern Island is treeless and sparsely vegetated. The yellow patagial tags contrast sharply with the birds' black wings, and 94% of on-island adults were perched rather than flying around the island during our surveys (Dearborn et al. 2001). The combination of these factors made detection of marked individuals very easy and allowed us to construct a season-long colony attendance history for these birds after their radio transmitters had been removed. On each survey of the colony, we recorded whether each tagged male was present at the colony and whether he was performing courtship display at that time. These season-long histories of individual males were summarized in two ways: the proportion of all survey detections on which a male was displaying (i.e., total display detections divided by total detections), and the actual number of surveys on which a male was displaying (adjusted for banding date, but not adjusted for how often a male was present on the island). Both of these measures excluded any days during which a male had an active nest with an egg or chick, as males have low testosterone during that parental care period (Chastel et al. 2005) and never display (Nelson 1975; Dearborn and Anders, unpublished data).

Pairing success was determined with these same twice-daily surveys of the island. Pair formation is a conspicuous multi-day process that involves a male and female sitting in physical contact with each other. Egg laying generally occurs 1 to 2 weeks after initial pair formation and nest building, and the male and female share in the 57-day incubation of the egg.

Data analysis

Linear regression models were used to test whether behavioral time budgets were predictive of energy expenditure. Because energy expenditure is related to air temperature in some bird species (e.g., Ellis et al. 1995), we also used regression analysis to test whether proportion of time spent in apparently heat-related postures was related to local weather conditions. Assumptions of normal residuals and constant error variances were confirmed for all regression analyses. A Mann-Whitney U test was used to compare the relative cost of courtship for preferred males (i.e., those subsequently chosen by females and thus inferred to be of high quality) and non-preferred males (those not chosen by females and inferred to be of low quality). For each male, we divided the FMR estimate by the proportion of the 2-day

time budget period that the male spent in courtship display, yielding a measure of energy spent relative to proportion of time spent displaying. One male who never displayed was excluded, as this created an infinitely large relative cost of display.

Rank correlation analysis was used to test for relationships between proportion of time spent on courtship behavior during our focal observations and proportion of time spent on courtship behavior by these same study individuals during the scan-sample colony surveys over the remainder of the breeding season. Logistic regression was used to test whether male pairing success was predicted by proportion of time spent in courtship behavior.

For the linear regression of field metabolic rate versus proportion of time spent on courtship, we conducted post-hoc power analyses according to Neter et al. (1989), using the following values from our initial analyses: the residual error term (MSE), the sum of the squared deviations in the predictor variable, and the degrees of freedom. With an alpha of 0.05, we used these parameters to estimate the probability of detecting a linear relationship of a particular slope. We calculated power for an array of different slopes that were based on hypothetical FMR ratios of the males that were observed displaying during 100% of our time budget observation and the male that displayed during 0% of our time budget observations. In this manner, we calculated our power to detect true slopes that corresponded to FMR ratios ranging from 1.1 (i.e., the FMR of the 100% display was only 1.1× that of the 0% display) to 3.0 (the FMR of the 100% display was 3.0× that of the 0% display). This range encompasses a 1.83 FMR ratio observed in sage grouse (Vehrencamp et al. 1989). In that study, temperature-corrected FMR was positively related to the number of display struts performed per day ($r^2 = 0.695$), and the predicted FMR from the best-fit regression line was 1.83× higher for the male sage grouse that performed the most struts (900 per day) than for male sage grouse that performed no struts at all. For the Mann-Whitney test to compare preferred and non-preferred frigatebird males in the relative cost of display, we calculated a 95% confidence interval on the difference in relative cost between these two groups (Daniel 1990).

Results

Of the 17 birds that were initially injected with doubly labeled water, time budget data were successfully collected for 15 individuals. Data collection was incomplete for 2 of the 17 birds because they left the island during our observation period. One of those individuals (D76), after an aggressive interaction with another male, left the island at 1406 hours on 8 February, the second day of time budget observations, returning to the island the next afternoon (9 Feb); later in the season (16 April), this bird was seen on the island of Lisianski, 800 km away from Tern Island. The second bird (D87) left the island and disappeared from sight in a thermal at 1355 hours on 14 February, the first day of time budget observations, and did not return until

7 April. Because these two birds lack full time budget data and also could not be captured at the correct time for collection of the final blood sample, they are not included in the results presented here. For the remaining 15 individuals, we collected an average of 13 h 43 min (range 12:16–15:27) of continuous time budget data per individual, evenly split across the two days between initial and final blood sampling. This observation time comprised, on average, 58% of each bird's waking hours during the period covered by the DLW sampling.

Time budgets during focal sampling

During our 2-day time budget observations, males were frequently involved in courtship, preening, and sleep, with small proportions of time spent in aggression, flight, and heat-related behaviors (Fig. 1). Males spent an average of 29.5% of observation time in courtship, but there was substantial variation among individuals: 14 of 15 males displayed at least part of the time, 6 males displayed at least 20% of the time, and 2 males displayed non-stop during more than 13 h of observation. Overall, the coefficient of variation for proportion of time spent in courtship display by different males was 1.37. There was also fairly high variation in time spent in heat-related postures (CV = 1.99), time spent in aggressive behaviors (1.11), and time spent flying or out of sight (1.53), with less variation in time spent in comfort movements (0.57) or sleeping (0.89).

Courtship display most commonly included gular pouch inflation and erection of the iridescent nape feathers

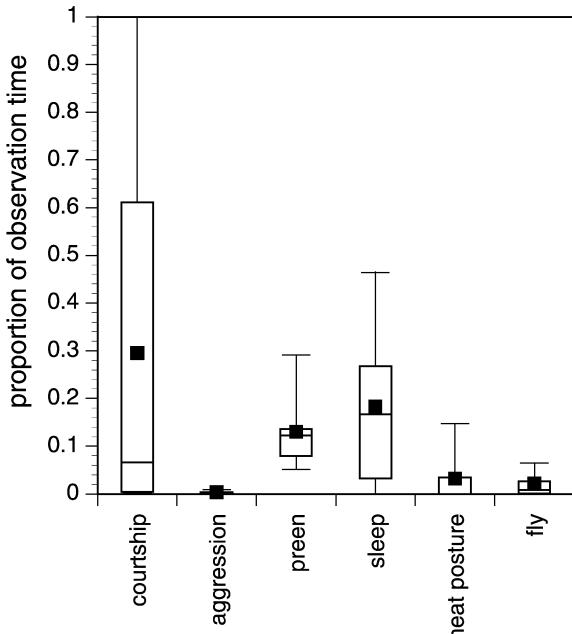


Fig. 1 Proportion of all observation time that males engaged in different behaviors. Categories are mostly, but not fully, mutually exclusive; for example, a male might preen while his gular pouch is inflated. Means are shown by squares, medians by horizontal lines, 25th and 75th percentiles by boxes, and 10th and 90th percentiles by whiskers

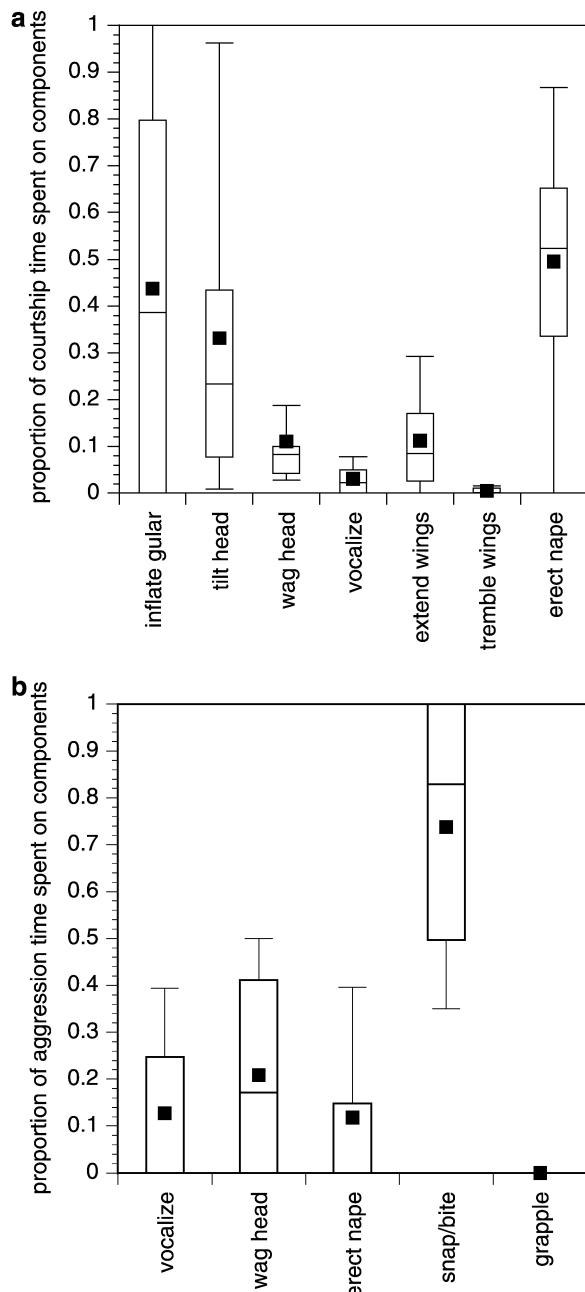


Fig. 2 **a** Proportion of display time that males engaged in particular components of the courtship display, and **b** proportion of male-male aggression time that males engaged particular components of aggressive behavior (symbols as in Fig. 1)

(Fig. 2a). Head wagging, wing extension, wing trembling, and vocalizations were relatively rare even within those periods characterized by other aspects of courtship display. These behaviors were typically performed only when a female was flying directly over the male's display site. When a mate-evaluating female was more distant (e.g., flying over a different group of males), the male was likely to remain in a less intense display that resembles a "ready" posture, with his nape erected, gular pouch inflated, and head tilted upward in an apparent attempt to scan for inspecting females.

Aggressive interactions between males were infrequent, accounting for an average of only 0.32% (range 0.01–1.26%) of the observation time for a given male (Fig. 1). Aggressive interactions often involved contests for abandoned nests, which males use (if available) as display sites. Aggression never escalated into full-grappling fights, instead consisting primarily of short bouts of bill-snapping and/or biting (Fig. 2b).

Thermoregulatory behaviors also constituted a small but variable portion of males' time (mean 3.27%, range 0.00–20.97%). The maximum and minimum weather values over the days and nights spanned by the DLW measures of the different males was 29.4 °C and 20.0 °C for air temperatures (T_a) and 44 and 0 km h⁻¹ for 2-min mean wind speed. The mean T_a during time budget observations for different individual males ranged from 23.3 to 25.0 °C, and mean wind speed ranged from 9.2 to 22.0 km h⁻¹. Despite this relatively narrow range of conditions, the proportion of time that different males spent in heat stress behaviors was negatively related to mean wind speed and positively related to mean air temperature during the period of behavioral observations (multiple regression, overall $F_{2,12} = 7.85$, $P = 0.007$, adjusted $R^2 = 0.495$; effect of wind speed: $t = -2.80$, $P = 0.016$; effect of temperature: $t = 2.37$, $P = 0.036$).

Energetic expenditure

For male frigatebirds that averaged 1.36 kg in body mass, energy expenditure during the 2 days spanning our time budget observations was 676.5 kJ/day (464.8–1,035.0), with CV = 0.22. There was little variation between individuals in body size (CV = 0.019 for wing length, and CV = 0.087 for mass), and there was no significant relationship between FMR and body size ($F_{1,13} = 0.28$, $P = 0.603$, $r^2 = 0.021$). Thus, the analyses below were conducted with unadjusted FMR estimates (i.e., total kJ/day), though the findings were qualitatively unchanged by using the residuals from the non-significant regression of FMR versus size rather than unadjusted FMR.

Field metabolic rate was not linked to behavior during the 2-day sampling period. In linear regression analyses, there was no relationship between FMR and proportion of observation time spent in courtship ($F_{1,13} = 0.01$, $P = 0.978$, $r^2 < 0.001$; Fig. 3), intense courtship (defined as sum of time spent wing-trembling, head-wagging, or vocalizing; $F_{1,13} = 0.09$, $P = 0.768$, $r^2 = 0.007$), aggression ($F_{1,13} = 0.06$, $P = 0.809$, $r^2 = 0.005$), flight ($F_{1,13} = 0.36$, $P = 0.557$, $r^2 = 0.027$), heat-stress behaviors ($F_{1,13} = 0.55$, $P = 0.473$, $r^2 = 0.040$), or sleep (here expecting a negative relationship; $F_{1,13} = 0.01$, $P = 0.938$, $r^2 < 0.001$). Equivalent results were obtained with multiple regression models. Excluding the one male who never displayed, preferred and non-preferred males did not differ significantly in their relative cost of display (preferred: median = 2,813.9, $n = 8$; non-preferred: median = 68,269.2, $n = 6$; $U = 13.0$, $z = -1.42$, $P = 0.156$; Fig. 4).

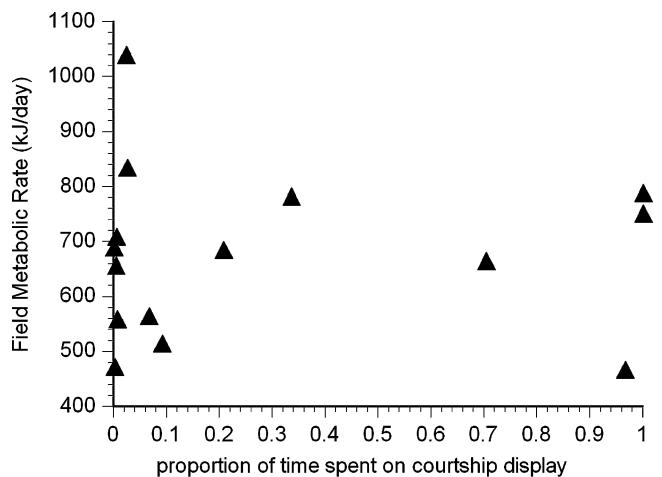


Fig. 3 Field metabolic rate (kJ/day) versus proportion of 2-day time budget that males spent on courtship display

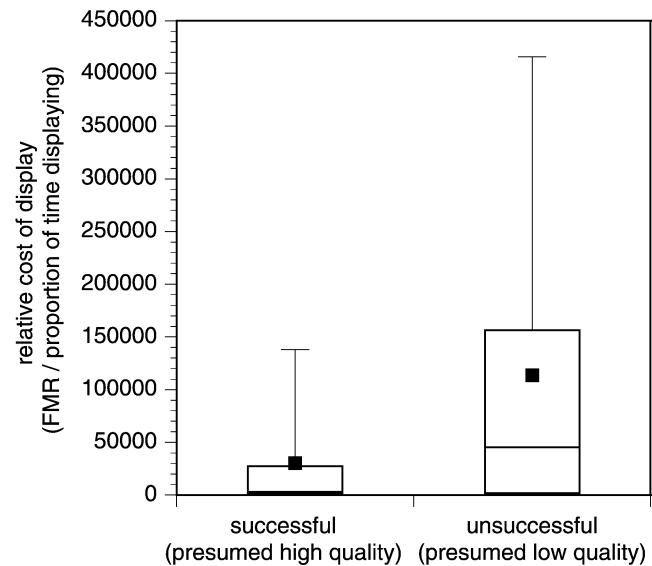


Fig. 4 Relative cost of display, expressed as field metabolic rate (kJ/day) divided by proportion of time spent displaying, for males that were chosen by females as mates that season (inferred to be *high-quality males*) and males that were not chosen as mates that season (inferred to be *low-quality males*). Means are shown by squares, medians by horizontal lines, 25th and 75th percentiles by boxes, and 10th and 90th percentiles by whiskers

In our regression analysis of FMR as a function of the proportion of 2-day observation time spent in courtship behavior, we had a power of 0.94 to detect a relationship of the strength seen in male sage grouse (1.83× change in FMR between non-displayer and most-displayer; Vehrencamp et al. 1989). We had a power of 0.8 (a value sometimes suggested as a good compromise with alpha) to detect a FMR versus courtship relationship in which males that displayed 100% of the time had a FMR that was 1.63× that of males that did not display at all. In the comparison of relative display cost (i.e., energy spent per proportion of time in display) for preferred versus non-preferred males, the 95% confidence interval on the difference in median relative cost for these two groups was -177,427.6 to 461.1;

thus the confidence interval spanned zero, and a small region in which preferred males would pay a greater relative cost than non-preferred males, and a large region in which preferred males would pay a lower relative cost than non-preferred males as predicted by handicap models.

Colony attendance, courtship, and pairing success

Over the course of the remainder of the breeding season, all 15 focal males spent the majority of their time away from the island. Between the date that we marked each bird (early- to mid-February) and the end of the survey period in early May, a given male was present on the island during 13.6% (range 4.9–20.3%) of surveys (excluding those surveys when a male was incubating an active nest). When not on the island, males are likely foraging pelagically, though many birds marked on Tern Island have been resighted briefly at colonies on other islands (Dearborn et al. 2003). Because the breeding population is large, there were always several hundred males on the island at any given time during the breeding season (Dearborn et al. 2001), despite the recurring absences of individual males as described here.

As noted above, males varied in the proportion of time spent on courtship behavior during our 2-day window of focal sampling in February. These males also varied in their subsequent involvement in courtship over the breeding season, as revealed by our twice-daily colony attendance surveys. Out of the total number of February to May surveys in which a given male was present on Tern Island, courtship displays were performed during an average of 36.0% (range for different males 0.0–74.1%) of those detections. The proportion of time that a male had performed courtship behaviors during our intensive 2-day time budget observations in February was positively correlated with two different measures of his subsequent courtship effort over the season: the proportion of all survey detections on which a male was displaying (Spearman's rho = 0.798, $n = 15$ males, $P < 0.001$), and the actual number of surveys on which a male was displaying (adjusted for banding date, but not adjusted for how often a male was actually present on the island; Spearman's rho = 0.671, $n = 15$ males, $P = 0.006$).

Males also varied in their success at attracting females, with 7 of the 15 males succeeding in attracting a mate. Two of those 7 males attracted a mate who subsequently laid an egg (comparable to the 15.8% of 76 wing-tagged but uninjected males that reached the egg-laying stage in the 2000 season; Dearborn and Anders, unpublished data). Both of those nests failed during the 57-day incubation period, and both of those 2 males resumed courtship displays; one did not attract a second mate, while the other did attract a second mate for a period of several days (though no egg was laid by that second female). The additional 5 males that attracted a mate either built or usurped a nest, but all 5 of those pairs dissolved without the female laying an egg. The remaining 8 males did not successfully attract mates on Tern Island in this breeding season. Male pairing success (i.e., did or did not attract a mate) was not significantly

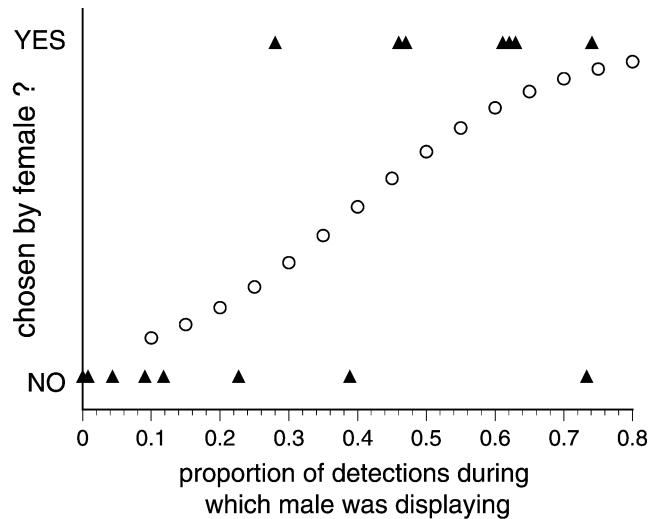


Fig. 5 Pairing success of individual males as a function of season-long display effort. Display effort is quantified here as the proportion of on-island detections that involved courtship display, where on-island detections are those twice-daily surveys during which the male was present on the island but not tending an egg or nestling. *Filled triangles* are observed data, and *open circles* are predicted values from the logistic regression

predicted by proportion of time displaying during our 2-day time budget observations (logistic regression: Wald $X^2 = 0.13$, $df = 1$, $P = 0.719$) but was positively related to courtship detections in our season-long surveys, whether measured by proportion of all survey detections on which a male displayed (Wald $X^2 = 4.53$, $df = 1$, $P = 0.033$, Nagelkerke $R^2 = 0.522$; Fig. 5) or by the number of surveys on which a male displayed (Wald $X^2 = 4.22$, $df = 1$, $P = 0.040$, Nagelkerke $R^2 = 0.753$).

Discussion

Male great frigatebirds varied substantially in the proportion of time spent performing courtship displays. This variation was apparent at, and correlated across, two temporal scales: during the detailed time budget observations that we conducted over a 2-day period for each male, and during the twice-daily snapshot checks of all males over the 3-month period of mate choice by females. During the 2-day time budget observations, courtship effort by individual males ranged from no courtship display at all to constant display during approximately 14 h of observation per individual. During the season-long surveys of colony attendance, individual males displayed during as few as 0% and as many as 74.1% of those surveys during which they were present at the colony.

Males that spent more time on courtship over the course of the mate choice season were more likely to attract a mate. Pressure on males to court females was previously suggested by the documentation of a male-biased operational sex ratio (typically five or six displaying males per mate-evaluating female at a given point in time; Dearborn et al. 2001) and by lower, more variable pairing success for

males than females (Dearborn and Anders, unpublished data). However, the link between courtship effort and pairing success had not been tested. Because courtship time was found to predict pairing success, handicap models of signal evolution predict that courtship would be costly. We did find large variation among males in proportion of time spent on courtship behavior ($CV = 1.37$) and in energetic expenditure ($CV = 0.22$, compared with mean $CV = 0.145$ for FMR values across breeding individuals within five other species of seabirds; Ricklefs et al. 1996). However, we did not find clear evidence that energetic expenditure provides a handicapping cost to male courtship. First, there was no linear relationship between FMR and proportion of time spent on display; such a relationship would have been expected under a handicap model if, as seen in sage grouse (Vehrencamp et al. 1989), males varied in their ability to recoup energy spent on courtship. Because we had high statistical power for detecting such a relationship, it is likely that this mechanism of the handicap process is not operating in this species.

The second handicap mechanism would be for low-quality males to spend more energy per unit of display time than high-quality males, such that low-quality males could not afford to display for as much time as high-quality males because they pay a higher per-unit cost. Note that this second handicap mechanism, contrary to the first mechanism, is consistent with the absence of a relationship between overall FMR and display effort. In our study, non-preferred male frigatebirds (i.e., those inferred to be of low quality) did not spend significantly more energy per proportion of time spent in display than did preferred males; however, the medians differed in the predicted direction (Fig. 4), and the confidence interval on the difference between the groups spanned a large range of values, most of which describe a higher per-unit cost for non-preferred males, as predicted by the handicap hypothesis. Thus, our test of the second handicap mechanism in great frigatebirds is equivocal.

There are at least three explanations for the lack of support for an energetics-based handicap on courtship display time. First, there may be energetic costs that are too small to measure over a 2-day time period. In the begging displays of nestling birds, most studies have found that the energetic cost of begging is a negligible component of the energy budget, even when measured with sensitive respirometry chambers (reviewed in Chappell and Bachman 2002); but in contrast, some studies have found evidence for a small growth cost of extended begging over a span of multiple days (Kilner 2001; Rodriguez-Girones et al. 2001; but see Kedar et al. 2000; Leonard et al. 2003). Similarly, frigatebirds could be paying a cost that is additive over a much longer time period (maximum recorded lifespan in this population is 43 years; Juola and Dearborn, unpublished data). A second possibility is that courtship display may be a handicap that is costly in currency other than energetic expenditure. Although predation risk is an important cost of courtship display in some species (e.g., frogs, Tuttle and Ryan 1981; guppies, *Poecilia reticulata*, Endler 1987), it is not a factor with frigatebirds, as they have no predators

at the breeding colony. But an alternate cryptic currency is immunosuppression, which could occur if display intensity is mediated by testosterone levels (Folstad and Karter 1992; Wedekind and Folstad 1994). And third, courtship display may not be a handicap signal at all.

Environmental conditions had some effect on male behavior but not on field metabolic rate. The 2-day time budget observations were made on different days for different males. Because we deliberately confined these observations to a 3-week period, the variation in ambient temperature and wind speed was relatively small, and male FMR was not related to mean temperature or mean wind speed during the observation period. The proportion of time spent in thermoregulatory postures, however, did vary with environmental conditions, as males spent more time in these postures when air temperature was high and when wind speed was low. This behavioral thermoregulation may have led to equivalent FMR by males under different thermal conditions. Alternately, the range of temperatures during our observations may have been narrow enough to remain thermoneutral for frigatebirds. In a climatic chamber study of brown noddies, *Anous stolidus*, from the Hawaiian Islands, oxygen consumption was parabolically related to air temperature, with the flat, bottom part of the curve spanning the temperature range seen during our time budget observations of frigatebirds (Ellis et al. 1995). This is consistent with the general view that thermoregulation during moderate weather conditions should contribute relatively little to FMR (Webster and Weathers 2000).

It is perhaps not surprising that other behavioral components of our time budget data were not predictive of FMR. Flight made up a very small portion of males' time budgets, and was expected to not be very costly; frigatebirds have extremely deep wings and low body mass, yielding the lowest wing loading of any bird and extremely energy efficient soaring flight, even compared with other seabirds (Weimerskirch et al. 2003). Aggressive behavior was also very uncommon and, as noted previously, many of the observed aggressive behaviors share components with courtship behaviors which were found to have little immediate cost. A more likely cost of aggression is the risk of escalation. Extensive fights, though very rare, have the potential to inflict serious damage. Protracted fights between males sometimes involve biting the opponent's gular pouch with the hooked tip of the bill, and we have observed a male unable to perform courtship displays due to a punctured gular pouch. We have also seen a fight between males lead to the loser being inextricably tangled in the dense, inflexible branches of a *Tournefortia* shrub; had he not been removed by field biologists he would have slowly starved to death. Although these incidents are rare, they have potentially severe consequences.

In general, seabirds are thought to have high FMRs compared to non-marine species, but these comparisons are limited to the breeding season and, more specifically, to the incubation period or to the period when parents are caring for young (Ricklefs et al. 1986; Nagy et al. 1999; Ellis and Gabrielsen 2002). Our measurements of FMR of frigatebirds, the first on a seabird during courtship, are difficult to

compare with other species because of lack of data. Compiling data for 37 species of seabirds from 3 different orders, mostly for parents caring for young or during incubation, Ellis and Gabrielsen (2002) described a relationship of $FMR (\text{kJ/day}) = 16.69 M(g)^{0.651}$, an equation that predicts a FMR of 1,829 kJ/day for a 1.36-kg frigatebird. Our estimate of 676.5 kJ/day for a frigatebird of this size during courtship is only 37% of the predicted value. Ellis and Gabrielsen (2002) also showed that FMR was correlated with latitude in seabirds. Their allometric equation that incorporates both body mass and latitude predicts a FMR of 1,268 kJ/day; our estimate is 53% of this value. If we compare frigatebird FMR during courtship to predictions of seabirds while continuously sitting on eggs (Williams 1996), we find that a 1.36-kg frigatebird would have a predicted metabolic rate of 565.0 kJ/day; our estimate of FMR during courtship is about 20% higher than this. Thus, our data suggest that the energy requirements of male frigatebirds during courtship may be relatively small. We do not currently know if frigatebirds also have a low FMR when they are caring for young.

In summary, we found that display time by male frigatebirds is predictive of pairing success, which raises the question of what prevents all males from displaying at a high rate. The natural history of this species suggests that an energetics-based handicap process is most plausible. We reject the most common form of energetic handicap, that the total energy spent by a male is correlated with time spent on courtship. Our results were equivocal, however, in testing an alternate mechanism, that high-quality males spend less energy per time spent in courtship than do low-quality males.

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