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Exploring hypotheses for sexual size dimorphism in frigatebirds

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ABSTRACT

Question: What selection pressures have led female frigatebirds to be larger than males?

Hypotheses: *Intersexual competition hypothesis*: Size differences are a result of selection for reduced foraging competition between the sexes. *Aerial agility hypothesis*: Size differences are a result of selection for increased aerial agility in males.

Species: Magnificent Frigatebird (*Fregata magnificens*).

Location: Barbuda, Lesser Antilles.

Methods: *Intersexual competition hypothesis*: We compared regurgitated prey, stable isotopes of blood, claw, and feathers, and foraging parameters of males and females. *Aerial agility hypothesis*: We explored the strength and direction of selection on wing traits that influence flight performance, using fledging success as a measure of fitness.

Results: *Intersexual competition hypothesis*: We found no differences between the sexes in breeding season diets or in foraging parameters. *Aerial agility hypothesis*: Females experienced strongest selection for larger bills and longer wings, while selection on males favoured a shorter wing measurement. We also found a negative relationship between male wing loading and nest size.

Conclusions: Manoeuvrability may help males win aerial contests over nest material. Selection for male speed or agility may be an important driver in small male size.

Keywords: aerial agility hypothesis, *Fregata magnificens*, frigatebird, intersexual competition hypothesis, resource division, selection gradients, sexual size dimorphism.

INTRODUCTION

Differences between males and females in size and shape are common among animals, and are thought to result from selective pressures acting differently on the two sexes (Price, 1984; Andersson, 1994; Fairbairn, 1997). While it is common for females to be larger than males among invertebrates, amphibians, and reptiles, males are the larger sex in most birds and mammals (Andersson, 1994; Fairbairn, 2013). Several main hypotheses have been proposed to explain such sexual size dimorphism [SSD (reviewed in Hedrick and Temeles, 1989; Shine, 1989; Andersson, 1994)]. The

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sexual selection hypothesis was first proposed by Darwin (1871) and predicts SSD when certain characters are favoured in one sex because they confer an advantage in mate acquisition. The conclusion that sexual selection is a major contributor to SSD through male–male combat or female choice is widely supported, at least in mammals, birds, and reptiles (Fairbairn *et al.*, 2007).

Different evolutionary optima in male and female body sizes may also arise via natural selection. For example, if males and females compete for resources, then each sex may benefit from avoiding extensive overlap with the other. Under this scenario, intersexual competition might be reduced by the evolution of different phenotypes (e.g. differences in body parts used in feeding) that facilitate the separation of foraging niches between the sexes (Selander, 1966; Shine, 1989; Andersson, 1994; Navarro *et al.*, 2009). A number of models (e.g. Lande, 1980; Slatkin, 1984; Reeve and Fairbairn, 2001) suggest that this *intersexual competition hypothesis* could play a role in the evolution of SSD in some taxa, particularly when the extent or direction of dimorphism cannot be fully explained by sexual selection. The *fecundity hypothesis* suggests directional selection on female size, via selection for larger individuals that are able to invest in greater numbers or quality of offspring or eggs (Selander, 1972; Snyder and Wiley, 1976). The *dimorphic niche hypothesis* attributes SSD to intrinsic differences in the reproductive roles of males and females (Darwin, 1871; Hedrick and Temeles, 1989; Andersson, 1994). For example, if there are differences between males and females because of different social roles or energetic needs for successful reproduction, there may be a different optimum body size in each sex (Slatkin, 1984; Weimerskirch *et al.*, 2009a). This hypothesis broadly describes inherent differences between the sexes, and as such could include several of the hypotheses described above (Hedrick and Temeles, 1989; Ruckstuhl and Neauhaus, 2005; Fairbairn, 2013).

These hypotheses are not mutually exclusive; multiple forcing factors often contribute to differences in optimal body size (Hedrick and Temeles, 1989; Shine, 1989). In addition, selection on one sex alone cannot account for SSD when there are genetic correlations between the sexes (e.g. Lande, 1980, 1987). Therefore, we chose one species – a seabird exhibiting female-biased SSD (females larger than males) – in which to explore hypotheses under natural and sexual selection pressures that affect size in both sexes to study the adaptive function and evolution of SSD.

Frigatebirds belong to a family of five closely related species of large, tropical seabirds that exhibit both strong female-biased SSD and colour dimorphism, making the sexes easy to distinguish. Males are ornamented with a red, inflatable gular pouch used in courtship displays, and a ruff of lanceolate, iridescent feathers (Nelson, 1975). Given their obvious ornaments, researchers have been interested in sexual selection in frigatebirds, but these studies have provided surprisingly little evidence of female preference for male ornaments (e.g. Dearborn and Ryan, 2002; Madsen *et al.*, 2007a, 2007b; Wright and Dearborn, 2009), so we turn our attention to other traits such as wing morphology.

We test multiple predictions for the evolution of SSD based on two hypotheses that seem plausible for the female-biased SSD in frigatebirds: the intersexual competition hypothesis and the aerial agility hypothesis (see below). We do not explicitly test the fecundity hypothesis, which generates predictions about female size and number or quality of eggs (but see Discussion). In seabirds, the constraints of returning to land to breed and low tropical marine productivity may contribute to general low provisioning rates of young, reduced clutch and brood sizes, and lower reproductive output (Ashmole, 1963; Gaston, 2004). Magnificent Frigatebirds (*Fregata magnificens* Mathews 1914) lay a single egg per season, have low fledging success, and the females provide parental care of the chick for over a year after the male abandons the nest (Diamond, 1972, 1973; Nelson, 1975; Osorno, 1999; Diamond and Schreiber,

2002). This low annual productivity creates difficulty for a short-term study to give fair treatment to the fecundity hypothesis. We also exclude direct tests of the dimorphic niche hypothesis, given its general nature and a lack of testable predictions.

Intersexual competition hypothesis

Magnificent Frigatebirds provide an appropriate case study for investigating the intersexual competition hypothesis, given the foraging challenges faced by tropical seabirds. Productivity in these marine ecosystems is typically low, and prey are patchily distributed (Ashmole, 1971; Longhurst and Pauly, 1987). Like many seabirds, frigatebirds feed near the surface and depend on other marine predators to bring prey within reach. Frigatebirds lack waterproof plumage and have small feet with vestigial webbing, and therefore avoid landing on water and feed primarily by aerial dipping (Nelson, 1975), taking mainly flying fish (Exocoetidae) and squid [Ommastrephidae (Diamond, 1975; Schreiber and Hensley, 1976; Weimerskirch *et al.*, 2004)]. Secondary modes of acquiring food include kleptoparasitism (stealing prey from other birds) and opportunistic feeding such as scavenging from fisheries, taking hatchling turtles, and snatching seabird chicks (Nelson, 1975; Calixto-Albarrán and Osorno, 2000; Diamond and Schreiber, 2002). Strong food competition is expected during the breeding season because thousands of breeding pairs often congregate at colonies and foraging range is restricted by the need to return to land to provision young (Ashmole, 1963; Lewis *et al.*, 2001). These factors presumably expose tropical seabirds to intense selection for efficient foraging (Ainley, 1977; Ballance and Pitman, 1999) and may, in turn, exert strong selection pressure for maintaining morphological and foraging differences (Weimerskirch *et al.*, 2006). In this study, we use a combination of diet and stable isotope analyses to test a prediction of the intersexual competition hypothesis: whether the longer bills and larger size of females result in their taking larger or higher trophic-position prey than males.

Resource partitioning may arise from differences in prey choice, foraging strategies, or distributions associated with morphological differences that segregate the sexes in space and time (Selander, 1966; Phillips *et al.*, 2011; Linnebjerg *et al.*, 2013). This leads to a second prediction of the intersexual competition hypothesis. It has previously been suggested that SSD, through the functional influence of mass and wing loading on flight performance, might affect at-sea distributions of frigatebirds (Harrington *et al.*, 1972; Diamond, 1975), and SSD has been linked to spatial segregation at sea in foraging albatrosses (e.g. Shaffer *et al.*, 2001; Phillips *et al.*, 2004). For example, under appropriate wind conditions a heavier female might glide faster than a lighter male with comparable wing area. Thus, sexual differences in morphology may favour the sexes exploiting different feeding grounds. We explore this prediction using GPS loggers providing high-resolution location fixes of foraging areas for male and female Magnificent Frigatebirds.

Aerial agility hypothesis

While the original sexual selection hypothesis is typically associated with larger males, in some cases small males may gain a fitness advantage (Payne, 1984; Jehl and Murray, 1986; Figuerola, 1999). For example, based on basic flight principles, there is an inverse relationship between predator mass and many aspects of aerial agility [e.g. linear acceleration and maximum horizontal speed in flapping flight, climbing rate, and the ability to initiate a turn quickly and to make tight turns all decrease with increasing mass (Andersson and Norberg, 1981)]. While

maximum sprint speed should decrease with increasing mass, other characteristic flight speeds such as the minimum power speed or the maximum range speed increase with total mass; however, for hunting or pursuit, sprint speed should be more relevant for success (Andersson and Norberg, 1981; Norberg, 1985). The aerial agility hypothesis predicts small male size in species where males perform acrobatic display flights (Jehl and Murray, 1986; Andersson, 1994). This hypothesis has primarily been applied to shorebirds and allies exhibiting female-biased SSD where female choice for acrobatic aerial displays may lead to smaller size in males (Jehl and Murray, 1986; Blomqvist *et al.*, 1997; Figuerola, 1999; Székely *et al.*, 2000, 2004; Sandercock, 2001). While frigatebird males display from perches rather than aerially, they are responsible for gathering nest material, which females fashion into a nest (Nelson, 1975). Branches and other vegetation used as nest material are a limited resource, are difficult to acquire, and are often stolen in flight or from unguarded nests (Diamond, 1972; Nelson, 1975) (Fig. 1). It has previously been suggested that the manoeuvres males engage in while attempting to bring nest material to their mate ('stick contests') make them good candidates for the aerial agility hypothesis, especially if smaller males are better at procuring nest material (e.g. Jehl andd Murray, 1986, p. 52). Frigatebird nests are somewhat insubstantial nesting platforms; eggs are sometimes lost over the edge when parents change over during nest relief, and nests may disintegrate during the nestling stage (Nelson, 1975). Larger, sturdier nests with more sticks likely reduce these potential hazards to nest success. We predict that traits associated with agility improve male frigatebirds' ability to acquire nest material.

We test the aerial agility hypothesis for the evolution of female-biased SSD using general flight principles to make predictions regarding the form of selection acting on wing traits that influence flight performance. Frigatebirds have notably low wing loading (mass/wing area) and high aspect ratio (wingspan^2/wing area) wings (i.e. long and narrow), traits that facilitate soaring great distances in search of food (Pennycuick, 1987). These wing traits also influence other aspects of flight performance; low wing loading is a major factor contributing to manoeuvrability, since turn radius scales negatively to wing loading (Norberg, 1985). Roll rate, another component of agility, is negatively correlated with aspect ratio. A shorter wingspan will lead to a decrease in wing inertia, allowing faster entry into and completion

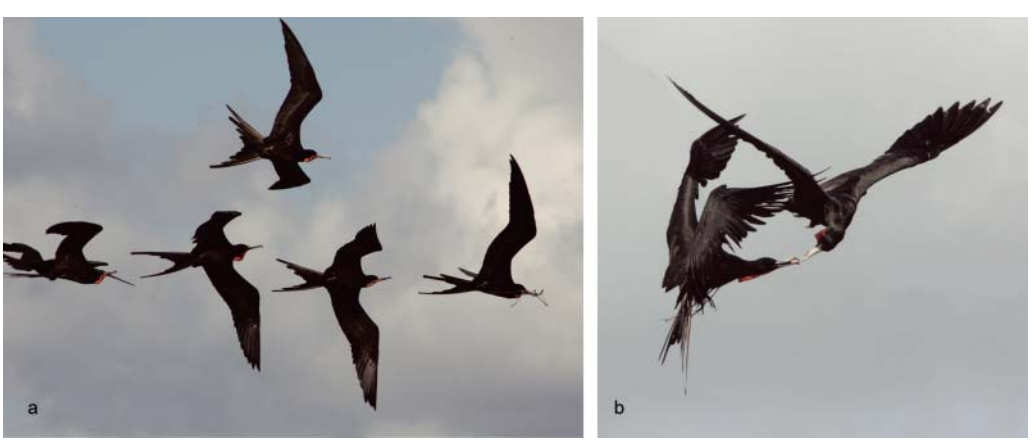


Fig. 1. Nest material contests by Magnificent Frigatebirds (*Fregata magnificens*) on Barbuda, Lesser Antilles. (a) Males chase another male returning to the colony carrying sticks. (b) Aerial 'tug-of-war' between two males competing for a stick (Photos: G.L. Holroyd).

of a roll (Andersson and Norberg, 1981; Norberg and Rayner, 1987). If more aerial males are better at procuring nest material, we predict that male wing traits associated with manoeuvrability (e.g. low wing loading and aspect ratio) will experience strong and differing selection compared with females. However, if flight efficiency is more important than agility, selection gradients should favour high wingspan and aspect ratios in both sexes. Selection on wing traits for aerial agility may occur through either directional selection or, more likely, through stabilizing selection at small values of aspect ratio and wing loading, given the likelihood of physiological constraints and other selection pressures at extreme values. We compare our predictions under the aerial agility hypothesis to the fitness surfaces of individual traits using fledging success as a measure of fitness.

Intersexual competition hypothesis: If SSD is a result of selection for reduced foraging competition between males and females, we predict that larger females should: (1) forage on larger/higher trophic-position prey than males, or (2) have separate foraging areas from males.

Aerial agility hypothesis: If SSD is a result of selection for increased aerial agility in males, we predict that: (1) selection should favour lower wing loading and lower aspect ratio in males than in females, and (2) the ability of males to collect nest material and the size of nests built should depend on wing loading and/or aspect ratio, with optimal values of the independent variables lower than the mean values found in females.

MATERIALS AND METHODS

We studied Magnificent Frigatebirds on Barbuda, West Indies (17°37′N, 61°48′W), a small (160 km^2), low-lying island in the Eastern Caribbean. Codrington Lagoon, on the northwest edge of the island, is semi-enclosed and ringed by mangroves (primarily *Rhizophora mangle* and *Avicennia germinans*), which provide nesting habitat for Magnificent Frigatebirds. The Barbuda breeding colony is likely the largest in the Caribbean (Diamond, 1973; Kushlan, 2009). Fieldwork was conducted during the main breeding period (November to March) in 2009–2012. Adult Magnificent Frigatebirds were captured by hand on their nests at night after dazzling them with a headlamp.

Intersexual competition hypothesis

Diet analysis

On capture or during handling, some birds regurgitated their last meal; these prey samples were collected in labelled plastic bags and frozen for later analysis. In the laboratory, frozen regurgitated samples were thawed and each prey item was blotted dry and weighed to the nearest one hundredth of a gram. We measured the length of individual prey items using vernier callipers: total and fork length for fish, or pectoral-tail length in the case of partial digestion (Murphy and Willis, 1996). For squid, we measured dorsal mantle (from mantle margin to posterior tip) and standard (from mantle to tip of arms) lengths. As the digested state of many samples precluded identification to species, we classified prey items into the following groups: flying fish, squid, other fish species (identifiable but present in low numbers), and unidentified fish (unidentifiable species excluding flying fish).

We tested for sex differences in prey composition using non-metric multidimensional scaling (NMDS) followed by PERMANOVA [permutational multivariate analysis of variance using distance matrices (Anderson, 2001)] with 1000 permutations and the Bray-Curtis dissimilarity index, using the metaMDS and adonis functions respectively, in the vegan package for R (Oksanen *et al.*, 2013). We compared the total mass of regurgitated prey between the sexes using a Mann-Whitney *U*-test. To compare the total length of flying fish and the standard length of squid (measured directly or estimated from linear regression of partial lengths) between the sexes, we used linear mixed-effects models with individual bird as a random factor, using the lme function in the nlme package. R v.3.1.3 was used for these analyses (R Development Core Team, 2015).

Stable isotope analysis

In pelagic seabirds, ^{13}C isotope signatures have been shown to vary geographically, with relatively well-defined shifts in isotope signatures across frontal boundaries (Cherel *et al.*, 2000). In addition, in tropical surface-feeding seabirds, $^{13}C:^{12}C$ shows an increasing offshore-to-inshore gradient and can indicate foraging habitat (Hobson *et al.*, 1994; Thompson *et al.*, 2000). Therefore, foraging zones differing in isotopic composition will be reflected in differing $\delta^{13}C$ tissue values between the sexes. The heavy nitrogen isotope ^{15}N shows trophic enrichment [of 2.3‰ for bird blood (Caut *et al.*, 2009)] and can therefore indicate differences in diet composition. Variation in $\delta^{15}N$ values of seabird tissues can also reveal information about prey size, as $\delta^{15}N$ values of some fish and squid are thought to increase with size/age class due to foraging at higher trophic levels (Revill *et al.*, 2009; Kurle *et al.*, 2011).

We collected several tissue samples from each bird for stable isotope analysis: blood, claws, and feathers. To obtain a short-term reflection of the breeding diet, we sampled whole blood [reflecting diet assimilation over approximately 1–5 weeks (Hobson and Clark, 1992a; Bearhop *et al.*, 2002; Cherel *et al.*, 2008)]. Blood samples (up to 120 µL per bird) were taken by brachial venepuncture using a 25-gauge needle and heparinized microcapillary tubes. Claws reflect a longer period of integration of weeks to months, and as we sampled only the distal tip and therefore the oldest claw tissue, our samples likely reflect diet during pre-breeding in frigatebirds (Bearhop *et al.*, 2003; Hahn *et al.*, 2014). Small pieces (approximately 2 mm) of the distal tip of a claw from the second or fourth digit were removed using animal nail clippers and stored in labelled envelopes. Moult occurs during the non-breeding period (Diamond, 1973, 1975; Nelson, 1975; Howell, 2010; personal observations) and the isotopic composition of feathers reflects diet during this time (Hobson and Clark, 1992b; Cherel *et al.*, 2000; Bearhop *et al.*, 2002). Non-flight feathers were preferred for sampling, as trimming flight feathers likely impairs birds' flight. Therefore, in all years we sampled 2–3 adjacent, central upper back feathers from each bird. In 2010, we also removed a small section of the distal tip of primary (flight) feather P7 or P8 (whichever was less damaged or broken).

In the laboratory, we cleaned feathers and claws of surface oils using a 2:1 chloroform:methanol solution and dried them for 72 hours in a fume hood. We cut samples of feather vane and claw from the distal end using sharp scissors or a scalpel. Blood and muscle samples were freeze-dried for 24 hours, ground and homogenized with mortar and pestle. We weighed subsamples into tin cups for stable isotope analysis. For reference to frigatebird tissues, muscle samples of fish and squid were also freeze-dried, homogenized, and submitted for stable isotope analysis. Target weights of tissue samples were 0.22 ± 0.02 mg (in 2009–2010) or 0.40 ± 0.02 mg (in 2011–2012). No lipid extraction was conducted, as

preliminary analyses demonstrated low lipid concentration via C:N ratios (Table 1) in all tissues (Cherel *et al.*, 2005; Post *et al.*, 2007).

Tissue samples were submitted to the Stable Isotopes in Nature Laboratory (SINLAB) at the University of New Brunswick. Samples were converted to gases by combustion in either a Carlo Erba NC2500 or Thermoquest NC2500 elemental analyser, and analysed for $\delta^{13}C$ and $\delta^{15}N$ using either a Delta Plus or a Delta XP continuous flow isotope-ratio mass spectrometer (Thermo-Finnigan, Bremen, Germany). Stable isotope results are reported in the typical δ notation as parts per thousand (‰) relative to Vienna Pee Dee Belemnite for carbon and atmospheric air (N_2) for nitrogen. Isotope values were normalized using secondary standards: commercially available pure compounds (nicotinamide, acetanilide) and internal standards [bovine liver standard (BLS), smallmouth bass muscle standard (SMB)]. All of these standards were calibrated against IAEA primary standards (CH6, CH7, N2).

Table 1. Stable isotope ratios of carbon and nitrogen and mass ratio of carbon to nitrogen in tissues (blood, feathers, claws) of Magnificent Frigatebirds (*Fregata magnificens*) and their main prey (flying fish, squid) over three breeding seasons on Barbuda, Lesser Antilles

Breeding season	Tissue	Sex	*n*	$\delta^{13}C$	$\delta^{15}N$	C:N
2009	Blood	F	16	−16.04 ± 0.21	8.09 ± 0.23	3.49 ± 0.14
	Blood	M	17	−16.05 ± 0.26	8.12 ± 0.31	3.41 ± 0.09
	Body feathers	F	15	−15.65 ± 0.83	11.80 ± 2.00	3.37 ± 0.10
	Body feathers	M	16	−15.72 ± 2.45	13.03 ± 2.42	3.40 ± 0.04
	Claw	F	16	−15.58 ± 0.35	8.73 ± 1.98	3.32 ± 0.04
	Claw	M	16	−15.77 ± 2.23	9.75 ± 2.23	3.29 ± 0.07
	Flying fish		17	−16.35 ± 0.49	6.35 ± 0.75	3.19 ± 0.10
	Squid		11	−16.64 ± 0.34	5.19 ± 0.53	3.33 ± 0.18
2010	Blood	F	17	−16.27 ± 0.37	8.79 ± 0.36	3.36 ± 0.03
	Blood	M	15	−16.25 ± 0.23	8.67 ± 0.36	3.38 ± 0.02
	Body feathers	F	16	−15.68 ± 1.53	11.82 ± 1.73	3.31 ± 0.05
	Body feathers	M	16	−15.24 ± 1.53	13.81 ± 1.95	3.34 ± 0.08
	Primary feathers	F	33	−15.92 ± 1.51	11.70 ± 1.90	3.40 ± 0.04
	Primary feathers	M	31	−15.79 ± 1.59	13.53 ± 2.30	3.38 ± 0.06
	Claw	F	16	−15.37 ± 0.64	8.54 ± 1.59	3.23 ± 0.06
	Claw	M	16	−15.33 ± 1.14	10.65 ± 1.90	3.24 ± 0.06
	Flying fish		13	−16.45 ± 0.30	7.18 ± 0.93	3.21 ± 0.08
	Squid		7	−17.38 ± 0.78	6.09 ± 0.42	2.50 ± 0.23
2011	Blood	F	17	−15.96 ± 0.15	8.03 ± 0.23	3.22 ± 0.07
	Blood	M	17	−16.11 ± 0.28	8.01 ± 0.28	3.24 ± 0.07
	Body feathers	F	18	−15.35 ± 1.08	12.61 ± 2.08	3.18 ± 0.05
	Body feathers	M	18	−15.27 ± 1.67	13.18 ± 1.55	3.17 ± 0.04
	Claw	F	17	−15.21 ± 1.03	9.08 ± 1.91	3.14 ± 0.05
	Claw	M	18	−15.20 ± 1.60	10.49 ± 1.60	3.11 ± 0.05
	Flying fish		11	−16.02 ± 0.33	5.73 ± 0.39	3.13 ± 0.05
	Squid		4	−16.51 ± 0.20	5.28 ± 0.39	3.30 ± 0.04

Note: Welch's *t*-tests showed differences in male and female claw and feather $\delta^{15}N$ values (see main text). Values are mean ± standard deviation.

Measurements of standards across all runs were accurate and precise: the mean ± SD for nicotinamide (expected batch value: $\delta^{13}C = -34.52‰$, $\delta^{15}N = -1.71‰$) was $-34.23 \pm 0.15‰$ for $\delta^{13}C$ and $-1.77 \pm 0.11‰$ for $\delta^{15}N$ ($n = 30$), while BLS (expected batch value: $\delta^{13}C = -18.8‰$, $\delta^{15}N = 7.18‰$) had $\delta^{13}C$ values of $-18.70 \pm 0.09‰$ and $\delta^{15}N$ values of $7.22 \pm 0.09‰$ ($n = 30$). Within an analytical run, replicate samples produced a standard deviation of 0.12‰ for $\delta^{13}C$ and 0.11‰ for $\delta^{15}N$ ($n = 24$).

Initially, differences in $\delta^{13}C$ and $\delta^{15}N$ (multivariate dependent variable) between males and females were tested for each tissue type using PERMANOVA on Euclidean distances with 1000 permutations, with permutations constrained within each year (strata = year). When significant, we further explored sex differences with a Welch's unequal variances *t*-test of $\delta^{13}C$ and $\delta^{15}N$ separately, pooled across years.

Foraging trips

To obtain data on foraging trips, we outfitted nine females and seven males with 13-gram GPS loggers with a Bluetooth remote download option, programmed to take a location every 2 hours (MicroTraX Pathfinder BT supplied by Axiz Ltd., Glasgow, Scotland). The remote download allowed us to obtain data for at least one foraging trip per individual, even if birds could not be recaptured for tag removal. GPS loggers that were 1.0% and 0.9% of male and female mass, respectively, were attached to the inner tail (rectrix) feathers with Tesa tape (acrylic-coated cloth tape in black, #4651 from Matco Packaging Inc., St. Laurent, Quebec, Canada), and were removed by recapturing birds after 1–2 weeks when possible (9 out of 16 birds).

As we tracked some individuals over multiple foraging trips, we used mixed-effects analysis of variance (ANOVA) to test for differences in male and female foraging. Flight speed, range (maximum distance from the colony), and distance covered were included in models as dependent variables, trip segment (outward vs. return trip) and time (day vs. night) as fixed factors, and year (2010, 2011, 2012) and individual as random factors using the nlme package for R (Pinheiro *et al.*, 2015).

To gain further insight into patterns of SSD in Magnificent Frigatebirds, we briefly explore trait allometry – the scaling pattern relating trait size to body size – in culmen (bill length measured along the dorsal ridge of the upper mandible) and wing traits. Relative trait size is constant for all body sizes in the case of isometry, decreases with body size ('negative allometry'), or increases with body size ('positive allometry'). A positive allometric trait is therefore larger in proportion to body size in larger individuals. The intersexual competition hypothesis would be supported by strong dimorphism, perhaps combined with allometry, in traits directly affecting foraging success (e.g. bill length) versus other structural body measurements (e.g. wing traits). Allometric relationships between morphometric traits were estimated using major axis (MA) regression with the R package lmodel2 (Legendre, 2014).

Aerial agility hypothesis

To measure phenotypic traits relating to predictions under the aerial agility hypothesis, during the 2009–2011 breeding seasons we captured adult Magnificent Frigatebirds on active nests (containing an egg or chick at time of capture) in mangroves at night. To follow nest fates, nests were marked with uniquely numbered metal nest markers attached with wire to a branch adjacent to the nest. We processed birds in a small boat in the shallow

water next to the colony and then returned them to their nests and ensured that they settled back onto their single egg or chick.

To test our prediction under the aerial agility hypothesis that the wing traits of males affect their ability to collect nest material, in 2010 and 2011 nest volume was estimated as a cylinder from nest depth and the mean of two measures of nest diameter taken at the time of capture using a measuring tape. A cylinder approximation for nest volume is suitable in frigatebirds, which make level platform nests, rather than the cup-shaped structures of songbirds.

Each adult handled (one per nest) received an aluminium North American Bird Banding Lab leg band. Birds were weighed to the nearest 10 g using a Pesola spring balance and with the bird placed in a pillowcase, the mass of which was subtracted from the total mass. Mass is often used for comparing sex-based size differences, but can fluctuate depending on body and breeding condition (Freeman and Jackson, 1990). Mass was usually measured without a 'payload', as birds that had fed recently tended to regurgitate their stomach contents on capture. At the time of handling, digital photos were taken of the bird's wing on a white background to measure semispan (distance from spine to wing tip) using the software ImageJ (Rasband, 1997–2012). Wingspan (calculated by doubling the semispan), wing area [total area of both wings including the region of the body between the wings; which supports the bird's mass when gliding (Pennycuick, 2008)], wing loading (mass/wing area), and aspect ratio [estimated as wingspan^2/wing area following Pennycuick (2008)] were later calculated from digital photos for each bird. Culmen (bill length, measured to the nearest 1 mm using vernier callipers) and natural wing chord (measurement taken with the wing bent at a 90° angle, from the most prominent point of the wrist joint to the most prominent point of the longest primary feather) were also measured at the time of handling.

We recorded fledging success as our measure of fitness. On Barbuda, nest initiation was asynchronous, usually between September and February. Nest status was assessed by one to four visits to marked nests after the initial capture, by walking through the colony and checking nests approximately every second month. Nest fate was unrelated to the timing of initial marking and subsequent nest checks (S.A. Trefry, unpublished data). The final nest check occurred just prior to fledging (usually May–July), as it was difficult to determine nest fate after a young bird had left the marked nest. Therefore, 'fledging success' was defined as a juvenile surviving to this point. Nests whose fate could not be determined were excluded from analyses (~10%).

To test the prediction that traits associated with agility might improve males' ability to acquire nest material, we initially explore the relationship between wing traits and nest volume, used here as an index of males' ability to collect and defend sticks. To assess the strength of natural selection acting on phenotypic traits of male and female Magnificent Frigatebirds, we used projection pursuit regression (PPR), which takes cross-sections (linear combinations of the original traits) of the fitness surface in the direction of strongest selection (Schluter and Nychka, 1994). Here, the fitness surface is the function relating reproductive success to phenotypic traits under selection. Projection pursuit regression is highly flexible in the surfaces represented, allowing estimation of directional, stabilizing, disruptive, and other forms of selection (Schluter and Nychka, 1994). This procedure is founded on the premise that selection does not act strongly on all phenotype dimensions, and we restricted our models to the single, strongest cross-section of the fitness surface by setting nterms = 1 in the ppr function (Schluter and Nychka, 1994; R Development Core Team, 2013). Morphological traits were standardized prior to PPR. To avoid problems with multicollinearity from highly correlated wing traits, we first tested the strength of selection on wing loading and aspect ratio, given

their known effects on flight performance. We then tested the strength of selection on remaining traits (e.g. wing chord, wing area, mass, culmen) to understand better selection on individual traits between the sexes. To visualize the form of selection acting on specific traits, we employed non-parametric regression (cubic splines) generated from generalized additive models (GAMs). The resulting fitness surfaces relate fledging success to traits that we predicted would be under strong selection under the aerial agility hypothesis. In addition to these visual methods, we computed quantitative selection differentials via linear models of covariance between standardized morphological traits and fledging success (following Lande and Arnold, 1983) and selection gradients (estimates of the strength of directional, stabilizing/disruptive, and correlational selection) via GAMs, following Morrissey and Sakrejda (2013).

The method of projection pursuit regression we used can be thought of as a non-parametric equivalent to logistic regression and is appropriate for our binary measure of fitness (fledging 'success' vs. 'fail'). We also used a binomial error structure with a logit link function in our GAMs. The smoothing parameter, which controls how closely the cubic spline curve fits to each of the data points, was chosen by minimizing the generalized cross-validation score. This is a measure of the overall prediction error associated with a given smoothing parameter (Schluter, 1988). These analyses were done using R v.2.15.3 (R Development Core Team, 2013). Splines were created using the mgcv package (Wood, 2006). The disruptive/stabilizing selection differential was estimated as the covariance between fledging success and the squared deviation of each trait. The significance of differentials was estimated using generalized linear models. Significant linear gradients indicate that selection favours either a phenotypic mean increase (if positive) or decrease (if negative). Selection gradients were computed using the gsg package (Morrissey and Sakrejda, 2012). Standard errors for selection gradients were calculated by bootstrapping, and our selection gradients should be regarded as exploratory rather than exact (Schluter, 1988; Morrissey and Sakrejda, 2013). Our prediction relating male wing loading to nest volume was tested using linear regression.

RESULTS

Sexual dimorphism is quite marked in Magnificent Frigatebirds; in our population, five of six morphological traits were significantly larger in females than males (Table 2). In our tests for allometry, the only significant regression between mass and a morphological trait was female culmen length (Table 3), which experienced negative allometry; smaller females had longer culmen lengths than predicted under isometry (Fig. 2). Other traits (wing area, wingspan) were not strongly related to mass in either sex; in particular, allometric relationships between male wing traits and body mass are lacking in our data (Fig. 2).

Intersexual competition hypothesis

Diet analysis

We collected 121 regurgitated prey samples (71 females, 50 males) from breeding adult Magnificent Frigatebirds. These samples were numerically dominated by flying fish (Exocoetidae), which comprised 63% of the diet for females and 76% for males. By biomass, flying fish comprised 67% and 73% of the female and male breeding diet, respectively. Squid represented 7% and 18% (by number), and 8% and 7% (by mass) of male and female diet,

Table 2. Summary statistics of measurements taken from breeding Magnificent Frigatebirds (*Fregata magnificens*) captured on nests on Barbuda, Lesser Antilles, 2009–2011

Variable	Females (*n*)	Males (*n*)	% Difference	*t*-test
Mass (kg)	1.47 ± 0.12 (75)	1.24 ± 0.10 (60)	15.6	$t = 12.08$, $\mathbf{P < 0.0001}$
Wing area (m^2)	0.37 ± 0.03 (63)	0.35 ± 0.03 (56)	4.6	$t = 2.90$, $\mathbf{P < 0.01}$
Wing loading ($g \cdot cm^{-2}$)	0.40 ± 0.04 (63)	0.35 ± 0.04 (56)	11.9	$t = 6.65$, $\mathbf{P < 0.0001}$
Wingspan (m)	2.10 ± 0.07 (61)	2.03 ± 0.06 (54)	3.0	$t = 4.75$, $\mathbf{P < 0.0001}$
Aspect ratio	12.04 ± 1.28 (60)	11.79 ± 0.65 (54)	2.1	$t = 1.43$, $P > 0.05$
Culmen (mm)	122 ± 5.0 (75)	110 ± 4.4 (60)	10.3	$t = 15.52$, $\mathbf{P < 0.0001}$

Note: % Difference indicates how much larger females are relative to males. *P*-values are Bonferroni corrected for multiple comparisons. See text for definitions of variables. Data presented as mean ± standard deviation (sample size). Significant *P*-values are in **bold** font.

Table 3. Major axis regression for allometry of log of morphological characters on the log of mass of male and female Magnificent Frigatebirds (*Fregata magnificens*) from Barbuda, Lesser Antilles, 2009–2011

Character	*n*	Slope	P-perm
Females			
Culmen	152	0.1405	**0.0099**
Wing area	97	1.0169	0.0891
Wingspan	96	0.0847	0.0594
Males			
Culmen	137	0.0575	0.0990
Wing area	91	−0.9638	0.2277
Wingspan	89	−0.0165	0.3861

Note: **Bold** font indicates significant regression.

respectively. We found no significant difference in prey composition between males and females (PERMANOVA: $F_{1,118} = 1.14$, $R^2 = 0.01$, $P = 0.325$; Fig. 3).

There was no difference in the total mass regurgitated by females (mean ± SD: 57.7 ± 49.1 g) and males (51.8 ± 36.3 g; Mann-Whitney *U*-test: $U = 1807$, $P = 0.562$). There was also no difference between the sexes in total length of flying fish (mean ± SD: for females 180.7 ± 67.1 mm, for males 176.9 ± 64.0 mm; mixed-effects model: $t = -0.26$, $P = 0.793$, d.f. = 46). While the higher percentage of squid by number (but similar percentage by mass) in female diets suggests males took larger squid, we found no significant difference in standard length of squid between females (mean ± SD: 88.2 ± 40.0 mm) and males (mean ± SD: 152.4 ± 41.7 mm; linear mixed-effects model: $t = 1.00$, $P = 0.334$, d.f. = 14).

Stable isotope analysis

We collected stable isotope samples from 180 females and 178 males (Table 1, Fig. 4). During the three breeding seasons of this study, males and females showed no difference in their overall blood isotopic ($\delta^{13}C$, $\delta^{15}N$) signatures (PERMANOVA: $F_{1,98} = 0.470$, $R^2 = 0.005$, $P = 0.452$). However, male and female claw isotope values from the pre-breeding

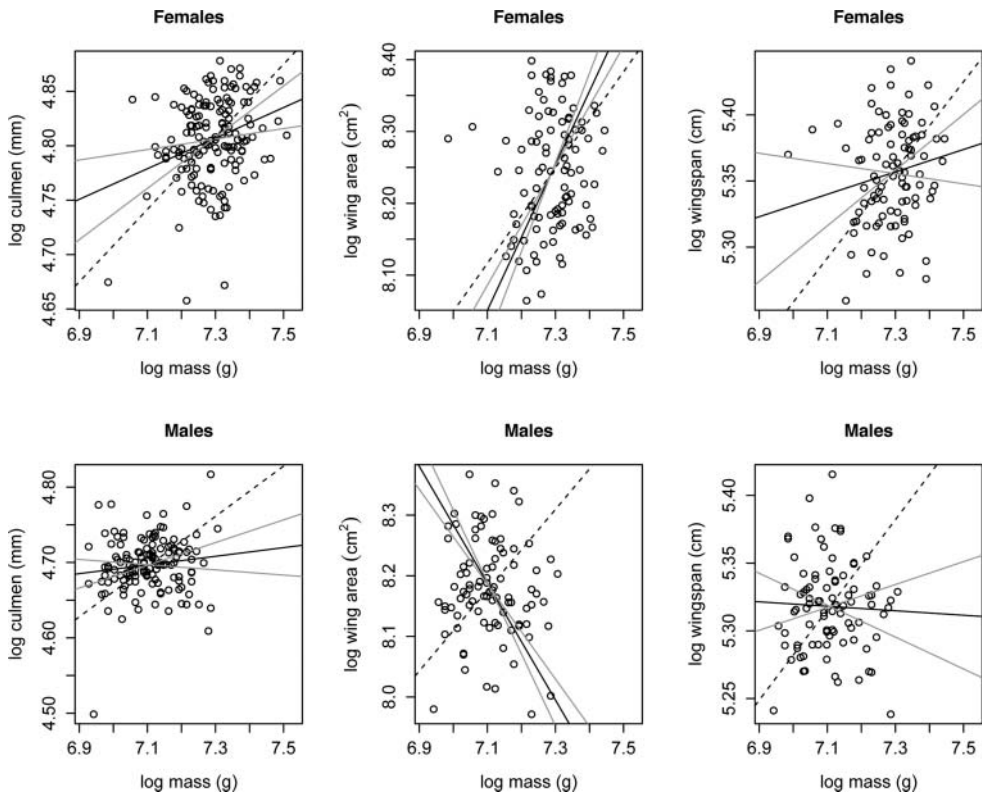


Fig. 2. Major axis regression lines (solid black lines) with 95% confidence intervals (solid grey lines) of bill and wing traits against mass of breeding Magnificent Frigatebirds (*Fregata magnificens*). Dashed line represents predicted relationship under isometry. All variables are log-transformed. Female culmen experienced negative allometry, while regressions of mass and other morphological traits were not significant.

season did show significant differences ($F_{1,93} = 11.675$, $R^2 = 0.112$, $P = 0.001$). Univariate analyses revealed segregation in $\delta^{15}N$ claw values (Welch's t-test: $t = -4.192$, d.f. = 93, $P < 0.001$) but not $\delta^{13}C$ values ($t = -0.048$, d.f. = 61, $P = 0.962$). The isotopic signatures from body feathers showed sex segregation ($F_{1,59} = 5.667$, $R^2 = 0.088$, $P = 0.004$), likely stemming from differences in source of diet outside of the breeding season. Further exploration again showed a difference in $\delta^{15}N$ body feather values ($t = -3.12$, d.f. = 59, $P = 0.003$) but not $\delta^{13}C$ values ($t = -0.411$, d.f. = 53, $P = 0.682$). Finally, isotope values of primary feathers also differed by sex ($F_{1,62} = 7.91$, $R^2 = 0.113$, $P = 0.002$), again due to $\delta^{15}N$ ($t = -3.465$, d.f. = 58, $P = 0.001$) rather than $\delta^{13}C$ ($t = -336$, d.f. = 61, $P = 0.738$) differences. The ratio of $^{15}N:^{14}N$ in tissues representing non-breeding season diet (claw and feathers) was consistently higher in males than females (Fig. 4).

Foraging

Nesting adults on Barbuda took foraging trips from the colony lasting 1.6 days on average (SD = 1.6 days, range 0.08–6.12 days; Fig. 5). Average day (13.1 $km \cdot h^{-1}$) and night (13.4 $km \cdot h^{-1}$) flight speeds were similar. Average outward flight speed was 10.1 $km \cdot h^{-1}$

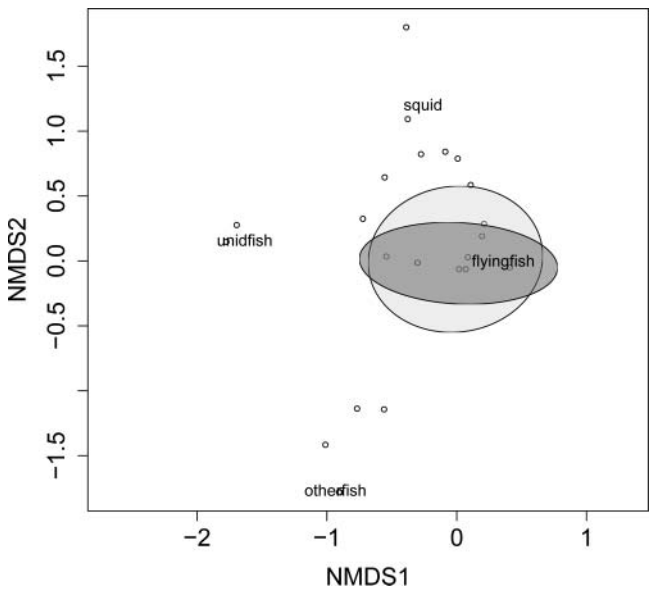


Fig. 3. Regurgitated prey types (flying fish, squid, other fish species, and unidentified fish) of breeding female (light grey ellipse, $n = 71$) and male (dark grey ellipse, $n = 50$) Magnificent Frigatebirds (*Fregata magnificens*) breeding on Barbuda, Lesser Antilles, from non-metric multidimensional scaling. Flying fish made up the greatest biomass and percentage by number of regurgitated items.

while average return flight speed was 21.7 $km \cdot h^{-1}$. The minimal adequate mixed-effects model with speed as the dependent variable revealed a significant effect of trip segment (outward/return) on speed ($t = 8.610$, d.f. = 613, $P < 0.001$), and an interaction between trip segment and time (day/night: $t = 4.451$, d.f. = 613, $P < 0.001$), such that the highest speeds were recorded on return segments at night (26.1 ± 15.3 $km \cdot h^{-1}$). Flight speed did not differ by sex ($t = -1.271$, d.f. = 12, $P = 0.228$). Sex also did not have a significant effect on foraging trip distance (523.5 ± 521.2 km, $t = -0.806$, d.f. = 14, $P = 0.434$) or range (202.0 ± 196.1 km, $t = -0.768$, d.f. = 14, $P = 0.455$).

Aerial agility hypothesis

Nest volume and wing traits

Under the aerial agility hypothesis, we predicted that male wing traits associated with manoeuvrability (e.g. wing loading, aspect ratio) would relate to nest size. Male wing loading explained a small proportion of the variance in nest volume ($F_{1,46} = 6.37$, $R^2 = 0.122$, $P = 0.015$), with a lower wing loading being associated with larger nests (Fig. 6). The relationship between aspect ratio and nest volume was not significant ($F_{1,46} = 1.10$, $R^2 = 0.023$, $P = 0.299$).

Strength and shape of selection: projection pursuit regression and cubic splines

In females, variation in fledging success was better explained by wing loading than aspect ratio, while the reverse was true in males (Table 4). Further exploration of traits via projection pursuit regression suggested that in males, wing chord followed by wing area

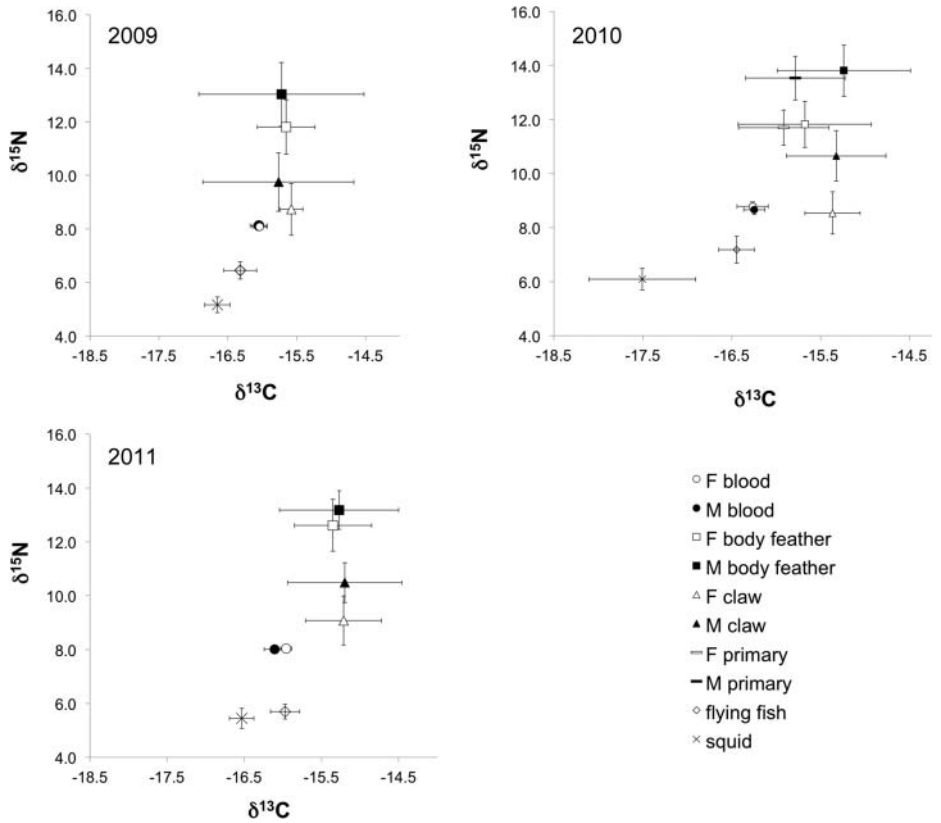


Fig. 4. Stable isotope (^{13}C and ^{15}N) ratios of tissue samples from Magnificent Frigatebirds (*Fregata magnificens*) captured on Barbuda, Lesser Antilles in 2009–2011. Error bars are 95% confidence intervals. Univariate analyses revealed significant differences in $\delta^{15}N$ from claws and feathers, representing non-breeding diet. See Table 1 for sample sizes.

Table 4. Direction of strongest natural selection of adult breeding Magnificent Frigatebirds (*Fregata magnificens*) from Barbuda, Lesser Antilles (2009–2011), from projection pursuit regression

Trait	Females ($n = 31$)	Males ($n = 27$)
Wing loading	**0.999**	–0.639
Aspect ratio	–0.006	**0.769**
Mass	0.343	–0.372
Wing area	0.087	–0.499
Wingspan	0.552	0.015
Wing chord	–0.198	**–0.774**
Culmen	**0.728**	–0.118

Note: Coefficients measure the contributions of each trait along the axis of strongest selection. Note that the sign indicates position along this axis, but not the direction of selection. Values of top contributing traits are in **bold**. Columns and horizontal line represent separate analyses.

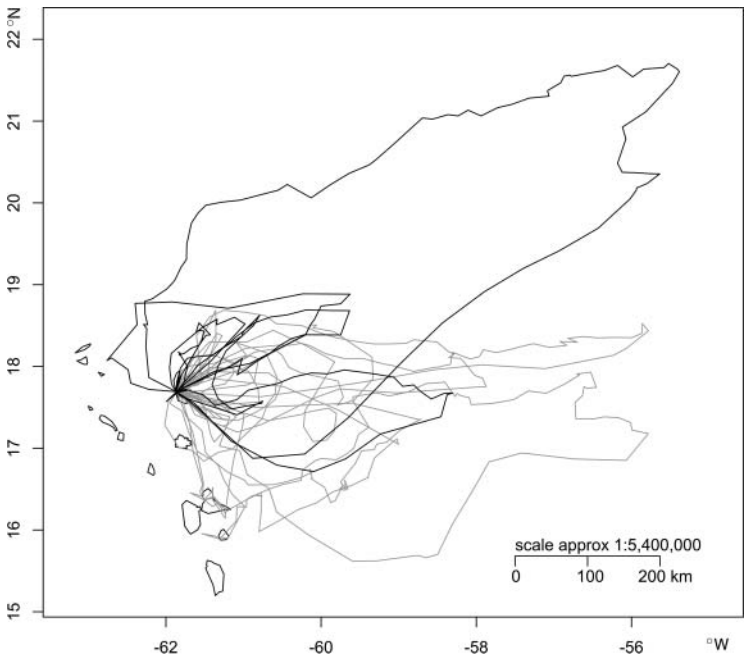


Fig. 5. Foraging trips of male (black) and female (grey) Magnificent Frigatebirds (*Fregata magnificens*) breeding on Barbuda, Lesser Antilles tracked by GPS loggers. Map creation: Brownrigg (2013), Brownrigg and Minka (2013).

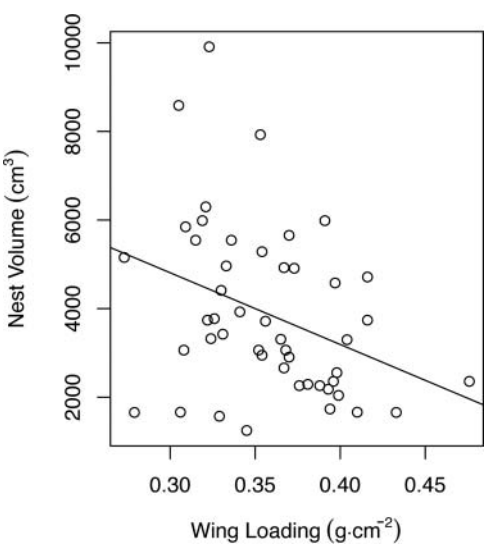
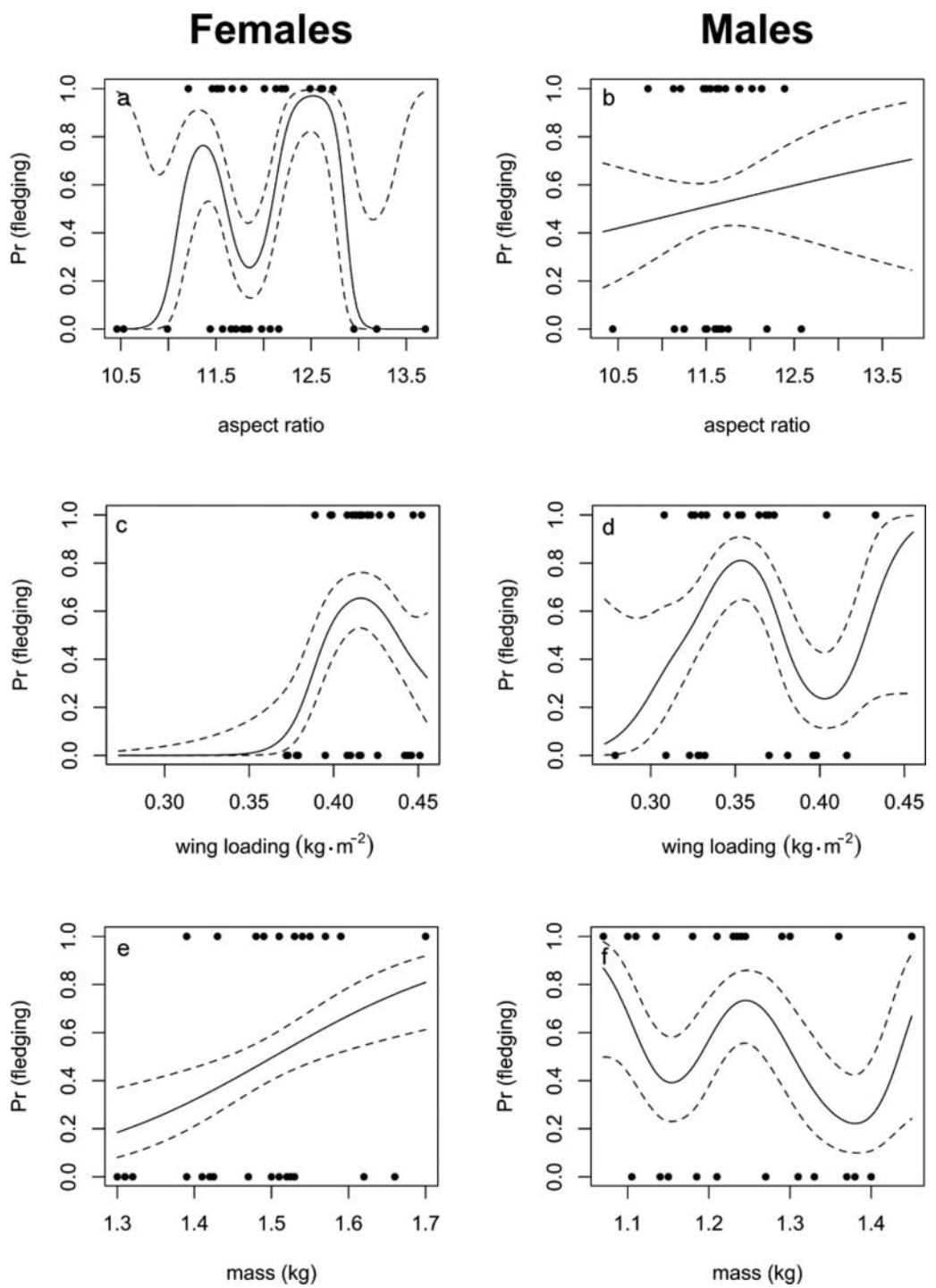


Fig. 6. Male Magnificent Frigatebird (*Fregata magnificens*) wing loading and nest volume (an index of males' acquisition of nest material) are negatively correlated, as predicted under the aerial agility hypothesis (linear regression: $F_{1,46} = 6.37$, $R^2 = 0.122$, $P = 0.015$). Measurements were taken from breeding adults on Barbuda, Lesser Antilles, 2010–2011.


Females
Males
a
b
c
d
e
f
Pr (fledging)
0.0
0.2
0.4
0.6
0.8
1.0
10.5
11.5
12.5
13.5
aspect ratio
0.30
0.35
0.40
0.45
wing loading (kg·m^{-2})
1.3
1.4
1.5
1.6
1.7
mass (kg)
1.1
1.2
1.3
1.4

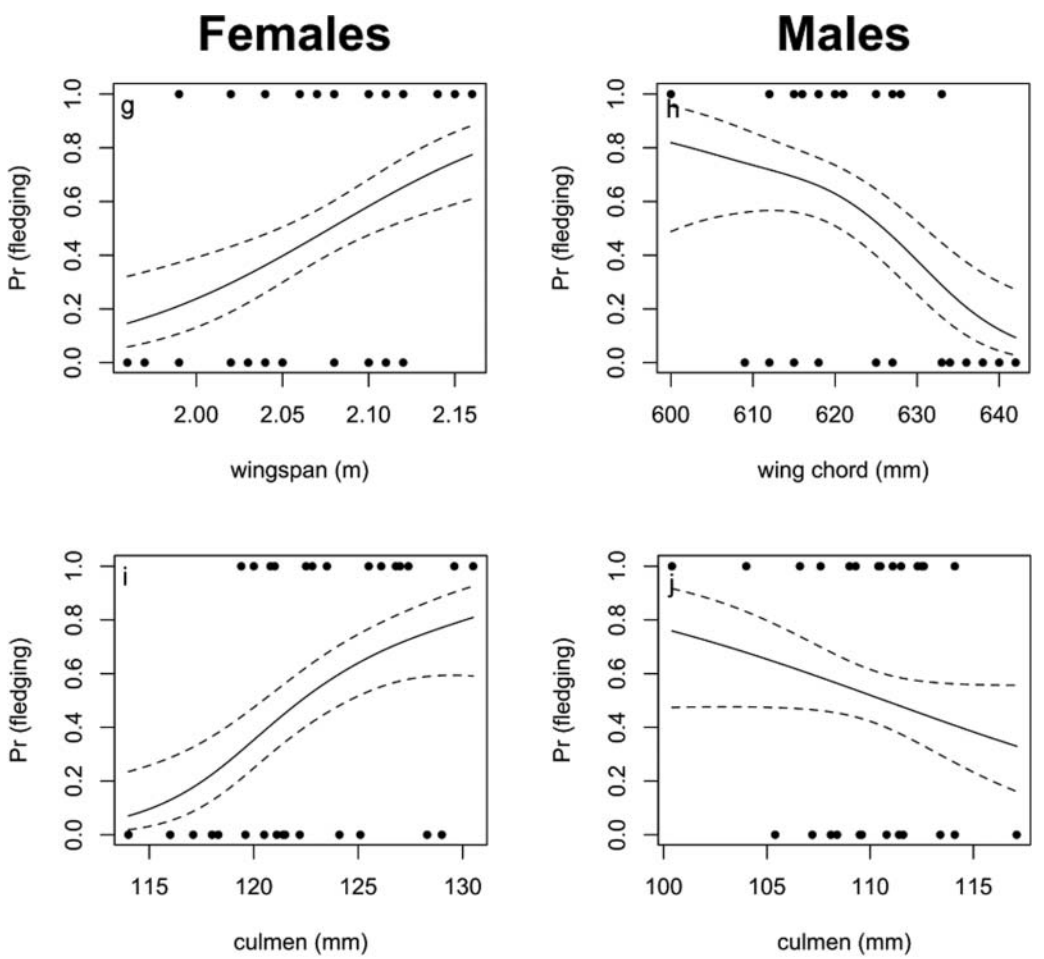


Fig. 7. Non-parametric estimates of fitness surfaces (as measured by the probability of fledging success) for mass and wing traits of Magnificent Frigatebirds (*Fregata magnificens*) measured on Barbuda, Lesser Antilles, 2009–2011. Dots indicate raw data points. Dashed lines indicate one standard error above and below the predicted line. Our estimates of directional selection gradients were significant for wing chord in males, and for culmen and wingspan in females.

experienced the strongest selection pressure. However, for females, culmen experienced the strongest selection, followed by wingspan and then mass.

In general, the cubic splines suggest differing selection on female and male traits (Fig. 7). For example, aspect ratio appears to experience positive directional selection in males but not in females (Fig. 7a,b). Mass appears to be under positive directional selection in females but stabilizing selection in males (Fig. 7e,f), and wing loading experienced stabilizing selection at higher values for females than for males (Fig. 7c,d). In females, wingspan appears to be under positive directional selection, while wing chord (a component of wingspan) experienced negative directional selection in males (Fig. 7g,h). Likewise, culmen was under positive directional selection in females, and negative directional selection in males (Fig. 7i,j).

Quantitative selection analyses

Due to small sample sizes and bootstrapping-based inferences, our calculation of selection differentials, selection gradients, and associated *P*-values cannot be considered exact. However, we include them here to lend interpretation to the qualitative analyses above. Selection differentials were strongest for female culmen, followed by wingspan and mass (positive), and we calculated significant stabilizing selection on female wing loading. In males, we detected significant directional selection on wing chord (negative) (Table 5). Due to power restrictions encountered by sample size, we limited estimation of selection gradients to aspect ratio and wing chord for males, and in two separate analyses for females, to aspect ratio and culmen, and wingspan and mass. For females, our estimates (±SE) of the slope of directional selection on culmen (0.389 ± 0.163, $P = 0.004$) and wingspan (0.262 ± 0.208, $P = 0.096$) were significant. For males, directional selection on wing chord was significant (-0.345 ± 0.158, $P = 0.018$).

DISCUSSION

Magnificent Frigatebirds exhibit strong female-biased sexual size dimorphism: females in our study were significantly larger than males in all phenotypic variables other than aspect ratio (e.g. 16% heavier). We also found negative allometry for culmen length in females, such that relative bill size decreased with body mass. We explore what these morphological differences can reveal about the importance of selection for diet segregation and aerial agility in frigatebirds, and briefly discuss other factors (e.g. energetic investment in reproduction) that could influence the evolution of female-biased sexual size dimorphism (SSD).

Table 5. Directional selection differentials (S_i) and stabilizing/disruptive selection differentials (C_{ii}) for morphological traits in a Magnificent Frigatebird (*Fregata magnificens*) population on Barbuda, Lesser Antilles

	Fledging success			
Trait	$S_i \pm$ SE	*P*	$C_{ii} \pm$ SE	*P*
Females				
Wing loading	0.073 ± 0.093	0.428	**−0.213 ± 0.082**	**0.024**
Mass	*0.158 ± 0.089*	*0.100*	−0.072 ± 0.069	0.304
Wing area	0.116 ± 0.092	0.213	−0.098 ± 0.069	0.190
Wing chord	−0.042 ± 0.094	0.650	0.011 ± 0.071	0.876
Wingspan	*0.177* ± 0.088	*0.065*	−0.013 ± 0.082	0.871
Aspect ratio	0.043 ± 0.094	0.640	−0.107 ± 0.058	0.120
Culmen	**0.207 ± 0.086**	**0.035**	−0.049 ± 0.084	0.554
Males				
Wing loading	−0.024 ± 0.102	0.809	−0.122 ± 0.091	0.205
Mass	−0.088 ± 0.100	0.374	−0.023 ± 0.105	0.823
Wing area	−0.121 ± 0.099	0.235	−0.072 ± 0.060	0.275
Wing chord	**−0.208 ± 0.093**	**0.049**	−0.093 ± 0.085	0.289
Wingspan	−0.096 ± 0.100	0.335	−0.139 ± 0.099	0.179
Aspect ratio	0.040 ± 0.102	0.683	−0.037 ± 0.062	0.545
Culmen	−0.091 ± 0.100	0.363	0.030 ± 0.060	0.612

Note: **Bold** font indicates significant differential; *P*-values ≤ 0.10 are in *italics*.

Intersexual competition hypothesis

Our study explores sexual segregation in foraging frigatebirds from several approaches: regurgitates, stable isotopes, and tracking data. Our in-depth exploration of foraging niche characteristics in Magnificent Frigatebirds allowed us to ask whether there is a possible ecological role for the evolution or maintenance of SSD in this species. Males and females showed no evidence of breeding season differences in prey type, size, trophic level, or foraging parameters. We did find evidence of isotopic niche segregation in the non-breeding season, but these differences were not consistent with our first prediction under the intersexual competition hypothesis.

A major assumption of the intersexual competition hypothesis is that prey capture should be a function of bill size (Selander, 1966; Shine, 1989). For example, in some species of diving cormorants and shags (Phalacrocoracidae), larger males take larger fish (Kato *et al.*, 1996; Cook *et al.*, 2007). Therefore, we predicted that female Magnificent Frigatebirds, with their longer bills, would take larger prey than males if SSD results from natural selection for resource division by prey size. We found no differences in the length of prey regurgitated by male and female frigatebirds. While stomach volume could be a constraint in smaller birds (e.g. Ricklefs, 1983), there was no difference in the total mass regurgitated by males and females. We also found no differences in the regurgitated prey of male and female frigatebirds breeding on Barbuda. Flying fish and squid were dominant prey types, as previously noted for Magnificent (Diamond, 1973; Nelson, 1975), Great [*F. minor* (Diamond, 1975; Weimerskirch *et al.*, 2004; Cherel *et al.*, 2008)], and Lesser [*F. ariel* (Diamond, 1975)] Frigatebirds. This reflects a diet based on direct fishing through surface dipping (Diamond, 1975; Schreiber and Hensley, 1976; Weimerskirch *et al.*, 2004). A previous study of Magnificent Frigatebirds during chick-rearing off the Mexican Pacific coast also found no significant differences in diet composition between the sexes, although the prey there was composed largely of prawn-fishery discards (Calixto-Albarrán and Osorno, 2000). Frigatebirds are notorious for kleptoparasitism, and sex-related differences in success rate or host size have been observed (Diamond, 1975; Nelson, 1975; Osorno *et al.*, 1992; Gilardi, 1994; Cummins, 1995). However, the opportunity for this foraging strategy near the Barbuda colony seems low, as there are very few other breeding seabirds on the island, and only small numbers of Brown Boobies (*Sula leucogaster*) come to roost in the colony in the evening (personal observation). Frigatebird piracy generally appears to have a low success rate, and may be an opportunistic foraging mode performed mainly near shore (Diamond, 1975; Nelson, 1975; Osorno *et al.*, 1992).

Stable isotope analysis of tissues grown over different seasons allowed us to investigate trophic niche partitioning in male and female frigatebirds across their annual cycle. We found no difference between males and females in isotope values of $\delta^{13}C$ and $\delta^{15}N$ in blood (representing diet assimilation while breeding). This lack of blood isotopic segregation was also found in Great Frigatebirds breeding on Europa Island, western Indian Ocean, Palmyra Atoll, central Pacific Ocean, and Ashmore Reef, Australia (Cherel *et al.*, 2008; Young *et al.*, 2010a; Mott *et al.*, 2017). The differences between isotopic signatures of flying fish and frigatebirds while breeding on Barbuda were consistent with the ^{15}N enrichment between fish muscle and seabird blood (Cherel *et al.*, 2005). However, we found differences between the sexes in the feather and claw tissues representing non-breeding diet assimilation. These differences stem from $\delta^{15}N$ values, indicating that outside the breeding season, males foraged on higher trophic-position organisms than females. While the differences are small (less than a trophic level), the trends are consistent across years and multiple tissue types. This finding is counter

to our first prediction of the intersexual competition hypothesis: given their smaller bills and body size, males were expected to forage for smaller prey with lower $\delta^{15}N$ values, particularly when breeding. However, trophic niche position may not necessarily always be size dependent (e.g. Layman *et al.*, 2005; Arim *et al.*, 2007). Mott *et al.* (2017) did find that non-breeding and early breeding season $\delta^{15}N$ values were higher in Great Frigatebirds than in smaller sympatric Lesser Frigatebirds, the ultimate mechanism likely being size differences. Male Great and Lesser Frigatebirds also had lower $\delta^{13}C$ values from feathers than female Lesser Frigatebirds, indicative of foraging farther offshore outside the breeding season (Mott *et al.*, 2017). Isotopic differences between the sexes in the non-breeding season may reflect behavioural differences that are unrelated to SSD, for example sex differences in nutrient requirements (e.g. Lewis *et al.*, 2002).

Phillips *et al.* (2011) found isotopic differences in seabirds with SSD were more common in the breeding season than in the non-breeding season, presumably reflecting greater between-sex partitioning when competition is greater. Studies from five taxa with male-biased SSD tended to show segregation in trophic level (males had higher $\delta^{15}N$ values), distribution (differences in $\delta^{13}C$ values), or both (Phillips *et al.*, 2011). In boobies (exhibiting female-biased SSD), evidence of isotopic segregation was mixed; some studies found differences between male and female tissues (blood, feathers) in $\delta^{13}C$ and/or $\delta^{15}N$ values (Cherel *et al.*, 2008; Young *et al.*, 2010a), while other studies did not find differences between the sexes (Weimerskirch *et al.*, 2009a; Young *et al.*, 2010b). These findings together with our own suggest that female-biased SSD in frigatebirds is not clearly associated with trophic position. Mancini *et al.* (2013) compared isotopic segregation by sex in tropical and non-tropical (temperate and polar) seabirds. From their literature review, 37 studies of 49 species showed intersexual foraging differences in $\delta^{15}N$ and/or $\delta^{13}C$ values. Temperate and polar species were more likely (71%) than tropical ones (19%) to show segregation by sex, although there were fewer studies on tropical species (Mancini *et al.*, 2013). In tropical marine environments, surface-feeding seabirds are strongly associated with larger predators such as tuna to make prey, predominantly fish and squid, available close to the surface (Ashmole and Ashmole, 1967; Au and Pitman, 1986; Spear *et al.*, 2007). This foraging strategy may equate to highly variable, low diversity prey, leading to the suggestion that SSD in the tropics may be more related to sexual selection or differences in reproductive roles rather than partitioning of feeding resources (Mancini *et al.*, 2013).

Sexual size dimorphism has also been broadly implicated in foraging segregation in seabirds through flight performance (e.g. Shaffer *et al.*, 2001; Weimerskirch *et al.*, 2009a; Phillips *et al.*, 2011). Differences in foraging behaviour between the sexes must be interpreted with caution, as sex-specific foraging performance may occur even in species with no sexual dimorphism (Gray and Hamer, 2001; Lewis *et al.*, 2002; Phillips *et al.*, 2004). However, given the relationship between wing loading, flight performance, and foraging area previously demonstrated in seabirds (e.g. Shaffer *et al.*, 2001; Phillips *et al.*, 2004), we explored whether foraging parameters differed between male and female Magnificent Frigatebirds during breeding. We found no differences in flight speed, trip distance, or foraging range between the sexes; neither did Weimerskirch *et al.* (2010) for Great Frigatebirds during incubation. Foraging areas around the breeding colony also highly overlapped between the sexes. This is counter to our prediction that heavier females might glide faster/forage farther due to their higher wing loading. Foraging in frigatebirds may be more constrained by wind speed, prey detection, or the need to return to the nest to provision the chick or relieve a mate (Pennycuick, 1987; Spear and Ainley, 1997). Studies of boobies suggest that even when there are sex-specific foraging behaviours, these do not

relate directly to morphology, and may be better explained by breeding investment or differences in breeding roles (Weimerskirch *et al.*, 2009a, 2009b). Our analyses of male and female foraging behaviour do not indicate segregation based on SSD near the colony.

Aerial agility hypothesis

Sexual selection for small male size in birds has most often been invoked in situations of aerial display. For example, a review of SSD in seabirds found that increasing male display agility correlated with evolutionary changes towards female-biased SSD (Serrano-Meneses and Székely, 2006). The authors concluded that sexual selection, through female choice for aerial males, influences female-biased SSD in seabirds. Acrobatic displays of males may also explain patterns of SSD in shorebirds and allies (Jehl and Murray, 1986; Figuerola, 1999; Székely *et al.*, 2004) and in bustards (Raihani *et al.*, 2006), and in a comparative analysis of over 30 avian families Székely *et al.* (2007) reached similar conclusions. Selection for small male size associated with speed and/or agility may also occur in a variety of contexts beyond display. For example, selection for small size and increased aerial agility for hunting small (and often more abundant) prey has long been suggested as an explanation for SSD in raptors (Storer, 1966; Newton, 1979; Pérez-Camacho *et al.*, 2015). Here, we review the evidence for our hypothesis that male contests over nest material may maintain small male size in frigatebirds.

Under the aerial agility hypothesis, we predicted strong selection for male manoeuvrability during contests over nest material, and therefore on male wing traits affecting flight performance. Frigatebirds are noted for having high aspect ratio wings and extremely low wing loading, traits that offer efficient soaring in search of food over large ocean expanses (Nelson, 1975; Pennycuick, 1983; Norberg, 1985). Exploring the strength of selection on these two wing traits via projection pursuit regression, we found the strongest selection on wing loading in females, and also on wingspan and mass. In males, aspect ratio experienced stronger selection, followed by wing loading. In addition, males with lower wing loading had larger nests. Because all birds were captured at a similar nest stage (when nest construction was largely complete), this finding supports our prediction that wing traits influence males' performance in stick contests. In quantitative selection analyses, we found evidence of significant stabilizing selection on female wing loading, and positive directional selection on female wingspan and mass. However, for males, we found significant directional selection on wing chord only; our calculations of selection differentials and selection gradients were not significant for wing loading. While these analyses do suffer from low power due to sample size limitations, it is also possible that the measured variation in nest size of breeding males in our population did not contribute significantly to variation in nest success.

Considering further selection on wing traits between the sexes – positive directional selection on female wingspan, and negative directional selection on male wing chord (a measurement that captures a component of wingspan) – leads us to conclude that some element of 'wing length' is under strong opposing selection in males and females. While it is difficult to directly link these morphological traits to flight function and performance, in general, longer wings are associated with soaring birds, and shorter wings with agility. Selection for smaller overall size, and in particular shorter elements of their wings, may be a result of selection for increased aerial agility in males compared with females. Selection on flight morphology for nest building represents a relatively short, but critically important stage in the annual breeding cycle, and in that way is similar to selection for acrobatic aerial

displays. Selection on males for shorter wings, in spite of the advantages of a high aspect ratio in soaring flight, may set males up for trade-offs in wing morphology between the breeding and non-breeding seasons. Complex locomotion such as flapping flight almost certainly incurs selection on multiple traits, and our study is an initial step in demonstrating strong selection on wing traits associated with agility in male frigatebirds.

Our analyses also demonstrated strong positive directional selection on female bill length, not found in males (if anything, male culmen was under negative directional selection). We discuss this finding below.

Other hypotheses for sexual size dimorphism

Female-biased SSD is sometimes explained by differences in parental roles or reproductive energy requirements. For example, under the fecundity hypothesis, large females are predicted to store and lay more or larger eggs, or have greater energy stores available for reproduction (Selander, 1972; Shine, 1989; Lindenfors *et al.*, 2007). Comparative analyses in reptiles and birds have found weak (or non-detectable) effects of female size on fecundity (Fairbairn *et al.*, 2007). However, in an exploratory analysis, we tested for a positive relationship between female mass (or structural measurements) and egg volume in Magnificent Frigatebirds. These relationships were not significant (e.g. for mass, linear regression: $F_{1,46} = 1.51$, $R^2 = 0.032$, $P = 0.23$). Another possible benefit is greater incubation ability of larger females (Snyder and Wiley, 1976). While this parental duty is shared in frigatebirds, other roles are not shared equally. Male Magnificent Frigatebirds abandon their mate and chick 19–160 days after the chick hatches, leaving the female to continue to feed the young for over a year (Diamond, 1972, 1973; Nelson, 1975). The extended period of chick provisioning provided by females might come with energetic consequences that result in selection for larger size. We found a significant positive directional selection differential for female mass. Magnificent Frigatebirds exhibit marked female-biased SSD and perhaps have the largest difference in parenting of the five species of frigatebirds (Nelson, 1975; Osorno, 1996). It would be interesting to explore whether differences in degree of dimorphism across the five species are dependent on different levels of biparental care relating to breeding energetics.

We predicted that females' longer bills might have allowed them to forage differentially compared with males. Our finding of allometry and fairly strong dimorphism (10%) in female culmen length suggests direct, differential selection on this trait. Indeed, our projection pursuit regression and quantitative selection analyses demonstrated strong, positive directional selection on female bill length (versus selection that appeared negative but was non-significant in males), and yet males and females had very similar breeding diets in our study. If not for foraging differences, differential selection on culmen length may result from other roles not directly tested here, such as nest defence. For example, while both sexes defend the nest and egg or chick, females might be more involved in deterring males attempting to pilfer nest material or usurp a nest site during the early stages of nest building and incubation.

In summary, we found no evidence of differences in diet or isotopic niche between male and female Magnificent Frigatebirds when breeding, in spite of the fact that females have longer bills and bill dimensions have often been suggested as an adaptation to different food resources (Selander, 1966; González-Solís, 2004; Navarro *et al.*, 2009). In addition, there was no difference in foraging parameters and foraging areas used by breeding males and females overlapped, in spite of the fact that females have higher wing loading than males, which has

been attributed to differences in foraging distribution in albatrosses (Shaffer *et al.*, 2001; Phillips *et al.*, 2004). We did find evidence of males foraging on higher trophic-position organisms in the non-breeding season relative to females. Since intraspecific competition should relax when individuals are no longer limited to central place foraging, these differences are unlikely to be the driving force behind the SSD exhibited by Magnificent Frigatebirds. Overall, we found no support for the intersexual competition hypothesis as a significant factor shaping SSD in Magnificent Frigatebirds. On the other hand, our tests under the aerial agility hypothesis demonstrated strong opposing selection on male and female wing length, associated with manoeuvrability and agility, and a link between wing loading and nest size in males. One possible explanation is that manoeuvrability helps males win aerial contests over nest material. This may be a result of sexual selection, natural selection, or a combination of forces if male manoeuvrability or agility factors into mate choice or winning male–male contests. Our evidence suggests that size dimorphism in frigatebirds stems from the very different reproductive roles of the two sexes. Selection for speed or agility leading to small male size may not be limited to the contexts of aerial displays or hunting ability, and could be a common selective pressure in other animals with female-biased SSD.

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