



A sex-influenced flexible foraging strategy in a tropical seabird, the magnificent frigatebird

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ABSTRACT: To successfully exploit resources, animals must be adapted to operate under phenotypic and environmental constraints. The strategies that predators use to locate prey are therefore diverse, particularly for breeding central-place foragers that must balance investment in reproduction and self-maintenance. Magnificent frigatebirds *Fregata magnificens* are tropical seabirds with intriguing morphology and feeding ecology, which display strikingly unequal levels of parental care (males deserting offspring months before females). These unusual traits can better help us understand the links between movement behaviour and breeding strategies in this poorly studied species. Using archival GPS, GPS-GSM loggers, bird-borne cameras and dietary data, we investigated the foraging ecology of chick-rearing magnificent frigatebirds from a breeding population in the Cayman Islands. This population engages in 2 main foraging strategies: (1) coastal trips over the continental shelf, where individuals target reef species and engage in kleptoparasitism, and (2) offshore trips during which birds feed on schooling pelagic prey. Differences in strategy use were partially linked to sex, with males (which invest less in offspring) roaming further from nests, and showing a higher propensity to forage offshore. Video data further indicated differences in social information use between strategies: foraging with conspecifics was more prevalent in coastal environments than pelagic. We suggest that observed variation in at-sea behaviour may partially be mediated by sex-based differences in parental roles, and/or size differences leading to intraspecific competition. Our study provides evidence of bimodal foraging and sheds new light on the importance of both pelagic and coastal feeding in this enigmatic species.

KEY WORDS: *Fregata magnificens* · Tracking · Seabird · Feeding ecology · Video logger

1. INTRODUCTION

Many breeding animals must balance the demands of offspring provisioning and self-maintenance, while functioning within phenotypic, energetic and geographical constraints (Trivers 1974, Ydenberg et al. 1994, McNamara & Houston 1997). To meet these challenges, species must adapt their foraging behaviour in ways that ultimately optimise both survival

and fitness (Trivers 1972, Nur 1988). Seabirds, for example, have developed a range of foraging strategies to locate often patchily distributed prey in ephemeral marine environments (Ricklefs 1990, although see Weimerskirch 2007). The diversity of morphologies and foraging strategies that have evolved within this group reflect the selective pressures at work within the wide range of environments exploited (Weimerskirch et al. 2002). The factors influencing an

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adult's choice of strategy are likely to be species- and location-specific, although body condition is believed to be a key determinant in some cases (Weimerskirch 1998).

One way that seabirds, as central-place foragers, have evolved to meet the demands of both chick provisioning and self-maintenance is to engage in flexible foraging, such as the alternating use of long and short trips (termed 'dual foraging'; Weimerskirch et al. 1994). Birds facing limited resource availability near the colony may, for example, supplement short trips in nearshore waters that maximise rates of chick provisioning with longer trips to distant rich foraging areas that allow restoration of body reserves (Cuthill & Kacelnik 1990, Weimerskirch et al. 1999, 2003). Such foraging strategies have been documented predominately in the procellariiforms (e.g. Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch 1998), with some reports amongst other groups of seabirds (e.g. sphenisciforms: little penguins, Saraux et al. 2011; Adélie penguins, Ropert-Coudert et al. 2004b; alcids: little auks, Welcker et al. 2009a, Brown et al. 2012; sulids: Ropert-Coudert et al. 2004a).

Variability in foraging behaviour within populations has also been attributed to sex-based differences in reproductive investment, physiology or other phenotypic attributes (e.g. Wearmouth & Sims 2008, Åkesson & Weimerskirch 2014, Cleasby et al. 2015). For seabirds, differences in parental roles that confer differing ties to the colony are believed to influence at-sea movements (Cristol et al. 1999, Welcker et al. 2009b, Pérez et al. 2014). Social dominance (often attributed to size dimorphism) can also result in competitive exclusion of one sex from profitable foraging areas (González-Solís et al. 2000, Marra 2000, Quintana et al. 2010). Similarly, size differences may influence aspects of flight such as aerial agility, allowing foraging niche divergence between the sexes (Shaffer et al. 2001, Weimerskirch et al. 2006a).

Here we studied the magnificent frigatebird *Fregata magnificens*, a wide-ranging tropical seabird that belongs to a genus of 5 closely related species with unusual life-history patterns (Nelson 1975). Frigatebirds tend not to coat their plumage in oil, preventing them from landing on or in the water without becoming waterlogged. Nevertheless, they travel extensive distances at sea during foraging and migration aided by low flight costs, and thus have a high dispersal potential (Pennycuik 1983, Spear & Ainley 1997, Weimerskirch et al. 2006b). *Fregata* species raise a single altricial chick per breeding attempt, have the longest reproductive period of any

bird and engage in extended periods of offspring provisioning (Diamond 1972, Osorno & Székely 2004). Nevertheless, they experience low rates of productivity (~20%, Diamond 1975, Osorno 1996). Marked reverse sexual dimorphism in frigatebirds (with females 26% heavier than males on average) has been linked to dramatically differing levels of parental investment between the sexes, with males deserting the chick months before female departure (~3 mo versus up to ~15 mo, Diamond 1972, Osorno 1999, Osorno & Székely 2004, Trefry & Diamond 2017). This unequal investment is thought to result in slow chick growth and breeding cycles that are annual for males but may be biennial for successful females (Diamond 1975, Hennenke et al. 2015). These traits make frigatebirds interesting candidates for investigating foraging strategies and the underlying drivers of variability in movement behaviour, since species with such extreme sex differences in parental roles might also be expected to show divergence in their at-sea behaviour.

Perhaps as a result of the intriguing lifestyles of frigatebirds, previous research has largely focussed on their breeding biology, diet, kleptoparasitic behaviour and energetics (Osorno et al. 1992, Carmona et al. 1995, Congdon & Preker 2004, Osorno & Székely 2004, Cherel et al. 2008, Mott et al. 2016). However, in recent years, the use of biologging has increased our understanding of their foraging behaviour such that movements during the breeding season have now been recorded in all 5 species. These studies have revealed high plasticity in their feeding strategies, ranging from surface and commensal foraging to scavenging and kleptoparasitism (Diamond 1973, Calixto-Albarrán & Osorno 2000, Weimerskirch et al. 2016). Similarly, variation and flexibility have been observed within and between species in the location and habitat types used during foraging. Foraging habitats are primarily oceanic (Weimerskirch et al. 2004, Hennenke et al. 2015, Mott et al. 2017), although coastal foraging has been suggested to be important in some cases (Weimerskirch et al. 2006b, Sebastiano et al. 2016). Some evidence of sex-based differences in habitat use in this group exists (Hennenke et al. 2015), although few studies have considered factors such as sex in the context of spatial movements (see Weimerskirch et al. 2006b, 2010, Trefry & Diamond 2017). Overall, fine-scale foraging movements, the use of different habitat types and links to breeding behaviour remain poorly understood. This is particularly true for magnificent frigatebirds, the only species in the family *Fregatidae* that breeds in the Caribbean Sea (Nelson 1975).

Using combined GPS, video and dietary data, this study provides a detailed investigation of foraging behaviour in magnificent frigatebirds. The main aims of the study were to (1) quantify the prevalence of nearshore versus pelagic foraging in this species during periods of chick provisioning; (2) investigate the influence of sex and chick age on patterns of foraging; and (3) explore drivers of within-population variability in foraging strategies.

2. MATERIALS AND METHODS

2.1. Study site and ethics

This study was conducted between March and June 2017 at a regionally important colony of magnificent frigatebirds within the Booby Pond Ramsar site on Little Cayman, Cayman Islands (19° 39.8' N, 80° 4.9' W; Fig. 1; estimated population size in 2017 = 654 breeding pairs, Hanlon 2017). All fieldwork was performed under permissions and guidelines of the Department of Environment, Cayman Islands Government, and National Trust of the Cayman Islands, and following established protocols to minimise disturbance (Guilford et al. 2008). All handling procedures were undertaken following ethical guidelines of the Universities of Liverpool and Exeter. To assess the potential impact of device attachment and han-

dling, breeding success (measured as the proportion of nests that hatched and fledged a chick) of all experimental nests ($n = 36$), and a group of closely matched unhandled control nests ($n = 163$), was recorded during the study. Fisher's exact tests were used to test for significant differences in breeding success between these 2 groups.

2.2. Tracking

Foraging movements of chick-rearing frigatebirds were tracked using solar-powered GPS-Global System for Mobile Communications (GSM) loggers (British Trust for Ornithology; mass = 26.0 g; mean \pm SD % of body mass = $2.2 \pm 0.3\%$), set to record fixes on a duty cycle of approximately 15 min and to transmit data via the mobile phone network once 12 locations had been logged. Birds were captured from their nests using a modified carbon-fibre extendable pole and monofilament nylon noose. Devices were attached to a small number of contour feathers on the backs of the birds using water-proof Tesa tape ($n = 22$: 11 females and 11 males), and birds were handled on average for 15 ± 5 min. Birds were released away from their nests to reduce disturbance to the chick, but were observed to return quickly. Owing to difficulties in capturing birds, these loggers were not retrieved, and when they ceased transmitting, they

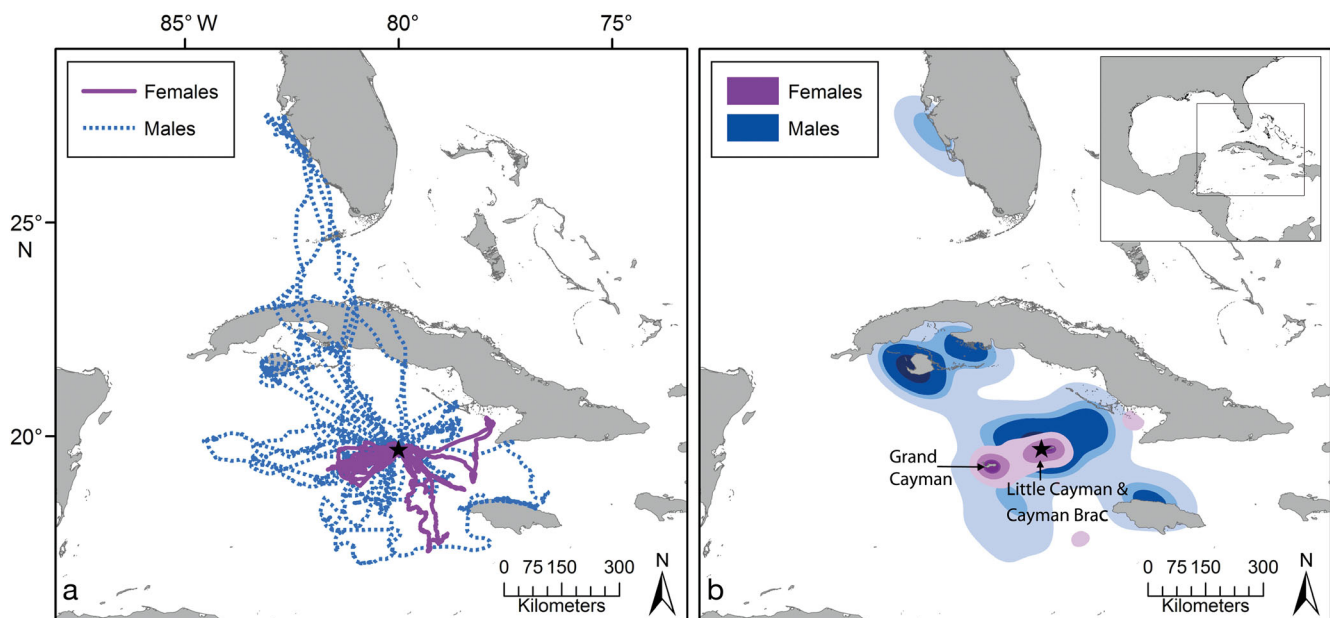


Fig. 1. (a) GPS tracks (10 min interpolated) and (b) kernel density estimates (25, 50, 70 and 90% contours) of hidden Markov model-assigned foraging locations from chick-rearing male (blue/dotted) and female (pink/solid) magnificent frigatebirds, tracked with remote and archival GPS loggers between March and June 2017 ($n = 22$). Star = colony location

were assumed to have been shed. Morphometric measurements (bill length, bill width, bill depth, maximum length of flattened wing cord, tarsus length and tail length) were taken from a subset of birds using Vernier callipers (± 0.1 mm) and steel rulers (± 1 mm) (for morphometric data, see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m611p203_supp/).

A small number of additional birds ($n = 20$) were tracked with archival GPS loggers (modified i-got GT-120, Mobile Action; mass: 15.1 ± 0.2 g), which were co-deployed with either video data loggers (Catnip Technologies; n : deployed = 4, recovered = 1) or tri-axial accelerometers (X8 or X16, Gulf Coast Data Concepts; n : deployed = 16, recovered = 3). GPS loggers were set to record positions every 30 s, accelerometers at 25 Hz and cameras set to record footage for 30 min every 1.5 h. Archival loggers were retrieved once birds were resighted at the colony (deployment duration: 1–14 d). The total mass of combined loggers did not exceed 3.8% of the bird's body mass (% of body mass: 3.2 ± 0.4). These loggers were retrieved using the same procedures as during tagging.

2.3. Data analyses

All GPS data were interpolated to 10 min intervals prior to analysis, using cubic piecewise hermite polynomials (following Tremblay et al. 2006). To identify behavioural patterns at sea, hidden Markov models (HMMs) were trained on GPS data comprised of a subset of foraging tracks from 15 individuals (n tracks = 15), using the HMM toolbox in Matlab (Murphy 1998), and then applied to the remaining tracking data (n tracks = 90). Models were fitted using $\log(x+1)$ -transformed ground speed and turning angle data (see Fig. S1, Tables S2 & S3 in Supplement 1). As the colony is set back from the coast, locations falling within 1 km of the colony were excluded to remove colony-based behaviours, and only full tracks were used in analysis (see the Supplement for further details). Probabilities from HMMs were then used to estimate the most likely behaviour at each time point in the tracks, allowing those locations likely to be associated with foraging behaviours to be extracted, and the proportion of time spent foraging per trip to be calculated. Model states were validated using behavioural information extracted from simultaneously collected video data for a GPS-tracked individual during the study. In brief, video frames were

analysed to provide an ethogram of 1 s intervals of at-sea behaviours, which allowed foraging activities (e.g. prey capture attempts or conspecific interactions) to be quantified with respect to strategy (see Table S4 for details).

Fixed kernel density estimates (KDEs) were calculated on all tracking data that were not used to train HMMs, after removal of trips lasting less than 30 min, locations falling over land (assumed to be resting) and locations classified as likely to be associated with sustained directed flight by the HMM (characterised by high speed and low turning angle, see Table S3; $n = 80$). Covariance bandwidth matrices were obtained using the least square cross validation estimator ('ks' package in R, Duong 2013) on projected coordinates to prevent spatial biases. We used 90% and 50% occupancy kernels to estimate the 'main' and 'core' home range area of the tracked population, respectively. For each foraging track, total distance travelled, maximum distance from colony, trip duration, mean distance from coast and home range areas (as above) were calculated. Foraging effort was also estimated as the proportion of trip time spent in foraging-related activities. These were defined from the most probable HMM state sequence to include State 3 ('foraging') and State 2 ('resting or searching') with points over land (assumed to be resting) removed. Unless otherwise stated, all data are presented as means \pm SD. Generalised linear mixed-effects models (GLMMs) with a gamma distribution, log link and random individual intercepts were fitted (Bates et al. 2013) to compare trip characteristics and foraging effort between (1) males and females, and (2) different stages of the chick-rearing period (early = chick ages 1–5 wk, late = chick ages 6–10 wk).

To identify and classify different foraging strategies, Gaussian mixture models were fitted on median distance from the coast and median trip duration values, following preliminary exploration of trip characteristic data. Bayesian information criteria for a series of candidate models with 1 to 9 states were used to determine the optimal number of clusters (see Fig. S2 and Table S5 for model outputs). The foraging efforts of birds engaging in coastal and pelagic strategies were then compared with linear mixed-effects models (LMMs) as above.

To determine the dietary habits of the study species, regurgitate samples were collected opportunistically from birds during tag deployment and recovery phases. Intact or partially intact (e.g. tail or head) prey specimens were later identified to the lowest taxonomic level with the aid of local fisheries experts.

Unfortunately, sample sizes were too small and unbalanced to allow for meaningful statistical analysis based on sex.

Statistical analyses were performed in R version 3.3.3 (R Core Team 2015), Matlab R2017a and ArcGIS version 10.3.1.

3. RESULTS

3.1. Impact of device attachment

We detected no significant difference in fledging success (proportion of eggs that hatched and fledged) of experimental and control nests (control, fledging success = 0.41, $n = 163$; experimental, fledging success = 0.53, $n = 36$; Fisher's exact test, $p = 0.196$, odds ratio = 0.615, power = 0.92).

3.2. At-sea behaviour and trip characteristics

We recorded 105 full foraging trips from 22 out of 42 tagged individuals (11 females and 11 males), 94 of which exceeded 30 min in duration and were used for further analyses (see Table S6 for logger deployment and recovery details). The tags recorded between 1 and 18 trips bird⁻¹ (mean = 4 ± 5), with logger transmission durations for GPS-GSM tags ranging between 1 and 64 d (mean = 18 ± 17). The remaining 4 GPS-GSM units failed before the birds departed the colony. The remaining 16 archival GPS units could not be recovered, because although the majority of birds were resighted at their nests, they evaded recapture (Table S6).

A comparison of negative log-likelihoods between candidate HMMs with differing numbers of states

provided support for a 3-state behavioural model (Fig. S1). The 3 states were characterised by (1) high speed and low turning angle (mean speed = $4.3 \pm 0.5 \text{ m s}^{-1}$, turning angle = $2.8 \pm 1.8^\circ$), (2) low speed and low turning angle (mean speed = $0.6 \pm 0.5 \text{ m s}^{-1}$, turning angle = $0.8 \pm 0.8^\circ$) and (3) low speed and high turning angle (mean speed = $0.7 \pm 0.7 \text{ m s}^{-1}$, turning angle = $25.0 \pm 2.8^\circ$). States were validated using observed behavioural patterns within simultaneously collected camera data: 81% of trip sections containing suspected foraging activity in the camera data were classified as state 3, providing strong support for the suggestion that this class is associated with foraging behaviour (Fig. 2; Table S3). State 1 was interpreted as being predominantly associated with sustained directed flight. State 2 was defined as 'rest or search' as it included periods of slow movement with low turning angles at sea (most likely associated with soaring and wind-driven movement) and other periods with 0 speed associated with resting on or near land.

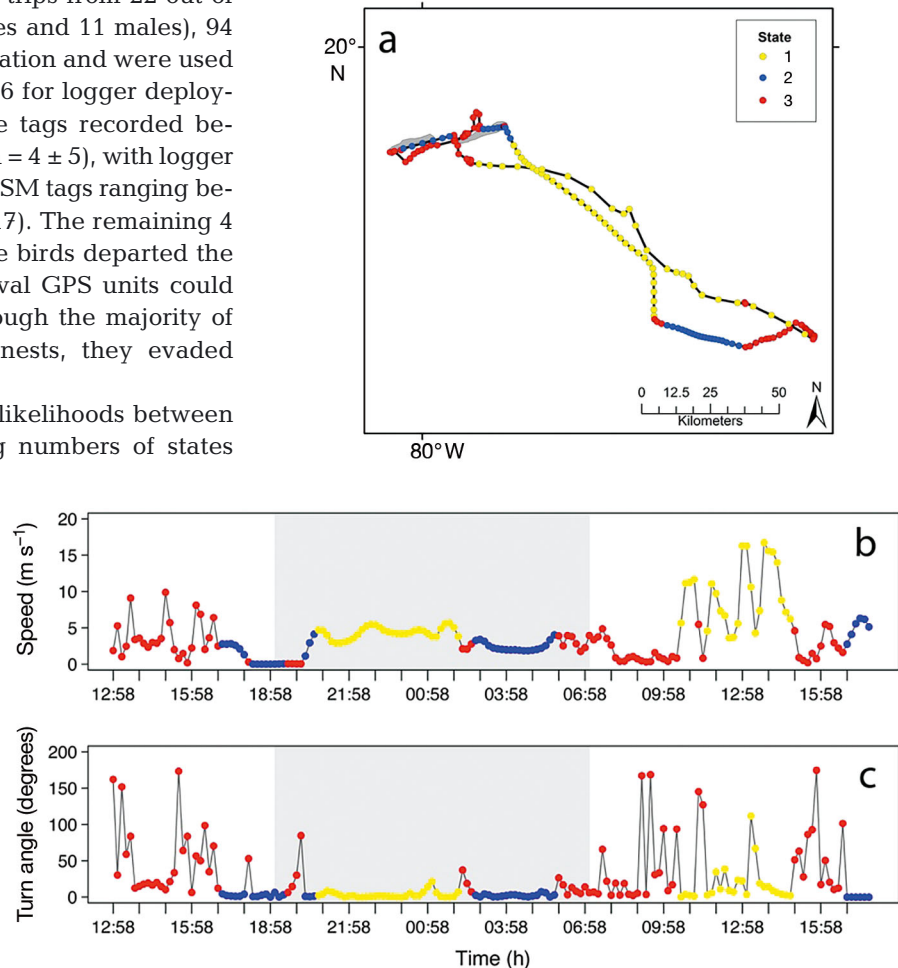


Fig. 2. (a) Example sections of a magnificent frigatebird foraging trip coloured according to assigned states from a 3-state hidden Markov model, and example time series of (b) ground speed and (c) turning angle coloured according to model-assigned states (yellow = state 1/sustained flight, blue = state 2/rest or search, red = state 3/forage). Grey shading indicates night-time hours

While many trips involved coastal movements around the Cayman Islands, birds also ranged extensive distances of up to 928 km from the nest, travelling as far as Florida, USA (Fig. 1). The foraging behaviour of male and female frigatebirds differed significantly, with males roaming significantly further from the nest and coastline, travelling greater total distances and engaging in longer trips than females, although no difference in foraging effort was detected (Table 1, Fig. 1). There was some evidence of sex-based differences in home range area (Table 1, Fig. 1), with females having smaller core home ranges. There was no evidence for differences in foraging trip metrics based on stage of chick rearing for either males or females (Table 1).

Three foraging tactics were identified using Gaussian mixture models, characterised by (1) commuting flights followed by coastal foraging activity in neritic waters off Grand Cayman, Cuba, Jamaica or Florida, USA, (2) pelagic trips of variable duration and (3) highly localised coastal foraging around Little Cayman and Cayman Brac (Fig. 3; Table S5). As strategies 1 and 3 both represented coastal activity, they were pooled for subsequent analyses, resulting in 2 main strategy classifications: coastal and pelagic. Of the 7 individuals (4 males, 3 females) tracked over more than 3 foraging trips, all engaged in both pelagic and coastal foraging. Females made more coastal trips (mean percentage of a female's trips that were coastal = 57 ± 40%), and males made more pelagic trips (mean percentage of a male's trips that were coastal = 43 ± 33%; Fig. S3), although no significant difference in the proportion of trips falling into the 2 strategies was detected between sexes (chi-squared test, $\chi^2_1 = 1.7$, $p = 0.195$). The presence of both coastal and pelagic feeding, and the importance of reef resources to the magnificent frigatebird population, was further supported by regurgitate samples, which contained both reef-dwelling and pelagic prey (Fig. 4). No significant differences in foraging effort were detected between birds that engaged in pelagic and coastal foraging strategies (LMM, least squares means of foraging effort: coastal = 0.676, pelagic = 0.648, $p = 0.701$).

Both coastal and pelagic foraging were observed in the individual tracked simultaneously with GPS and a video logger (Fig. 5; see Supplements 2 & 3 at www.int-res.com/articles/suppl/m611p203_supp/ for example video clips). A detailed analysis of video data provided preliminary evidence to suggest differences in the cues employed by individuals while engaging in coastal and pelagic foraging: there was a significantly higher incidence of conspecific and heterospecific interactions during coastal foraging than during pelagic trips (chi-squared test, $\chi^2_1 = 139.7$, $p <$

Table 1. Least squares means (±SE) from generalised linear mixed-effects models (GLMMs; with random individual intercepts), linear mixed-effects models (LMMs; with random individual intercepts) or linear models (LMs), fitted to compare trip characteristics of male and female magnificent frigatebirds tracked from Little Cayman with remote and archival GPS loggers during the chick-rearing period in 2017. Asterisks indicate significant ($p < 0.05$) differences

Parameter	Sex		Chick age (females)		Chick age (males)		p
	Female	Male	Young (1–5)	Old (6–10)	Young (1–5)	Old (6–10)	
n (birds/trips)	11/45	11/49	34	21	32	18	–
Max distance travelled from colony (km)	55.7 ± 10.1	156.1 ± 29.7	57.8 ± 13.1	53.1 ± 15.1	141.0 ± 34.8	183.1 ± 60.2	0.524
Distance to coastline (km)	10.5 ± 2.4	31.0 ± 7.2	68.9 ± 25.5	103.0 ± 30.4	337.6 ± 102.8	211.1 ± 85.7	0.356
Total distance travelled (km)	190.6 ± 35.6	471.2 ± 92.3	213.9 ± 49.6	155.1 ± 45.1	467.1 ± 119.3	478.5 ± 163.0	0.955
Trip duration (h)	2.2 ± 3.9	48.7 ± 8.9	22.7 ± 5.0	21.7 ± 6.0	55.4 ± 13.0	36.7 ± 11.5	0.292
Foraging effort (% time)	0.56 ± 0.06	0.56 ± 0.06	0.60 ± 0.08	0.45 ± 0.12	0.56 ± 0.05	0.55 ± 0.09	0.926
Core home range (km ²)	89.7 ± 222.2	1017.9 ± 3632.6	–	–	–	–	–
Main home range (km ²)	440.8 ± 3046.1	4297.1 ± 1350.4	–	–	–	–	–

^aGLMMs; ^bLMMs; ^cLMs

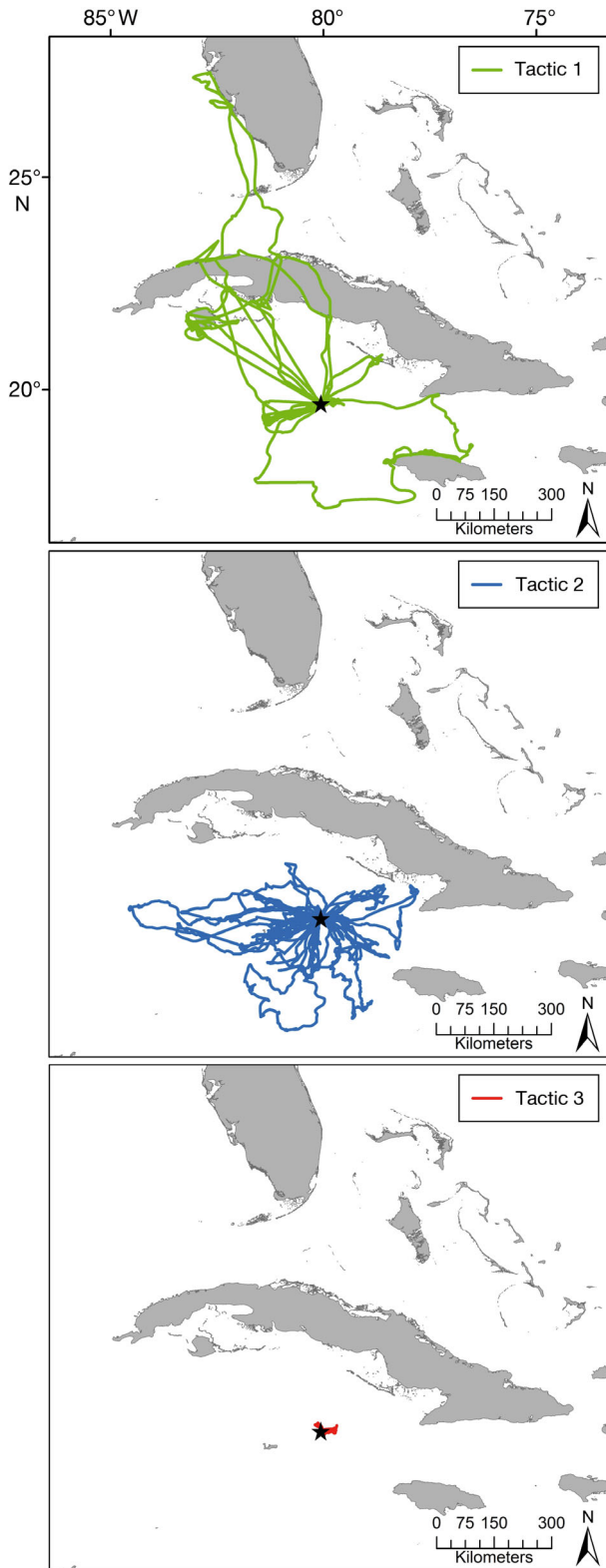


Fig. 3. Three foraging tactics classified according to a 3-component Gaussian mixture model fitted using 'distance to coast' and 'trip duration' metrics for foraging trips of GPS-tracked magnificent frigatebirds ($n = 22$) from Little Cayman, Cayman Islands, in 2017

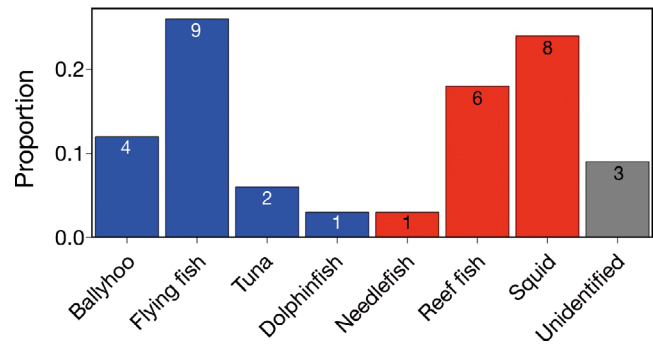


Fig. 4. Prey composition of regurgitate samples collected from magnificent frigatebirds ($n = 12$) during the tracking period between March and June 2017, showing the proportion of samples falling within each prey category. Blue bars = pelagic prey, red bars = coastal prey. Numbers on bars refer to recorded sample sizes within each prey category

0.001). Only one conspecific interaction was observed during pelagic foraging, and this appeared agonistic in nature as opposed to feeding-related (Fig. 5).

4. DISCUSSION

This study reveals new insights into the foraging ecology of magnificent frigatebirds, providing evidence for a bimodal foraging strategy, sex-based differences in foraging behaviour and the importance of both coastal and pelagic foraging. We discuss our results below in relation to breeding behaviour, intraspecific competition and sex-based differences in parental investment in the study species.

4.1. Flexible foraging strategies

All birds tracked over extended periods (>4 foraging trips) showed flexibility in foraging behaviour, engaging in both coastal and pelagic movements. While not previously described formally in frigatebirds (but see Sebastiano et al. 2016), such flexibility is not unexpected in tropical species such as this, which live in environments generally characterised by low productivity and resource predictability (Weimerskirch 2007). An ability to adapt to changing conditions and switch between different prey resources in tropical waters is therefore highly advantageous. The flexible strategies seen here are indeed consistent with a tendency for low levels of site fidelity and a low occurrence of area restricted search behaviour reported in the few tropical seabird populations studied to date (Weimerskirch 2007, Oppel et al. 2017).

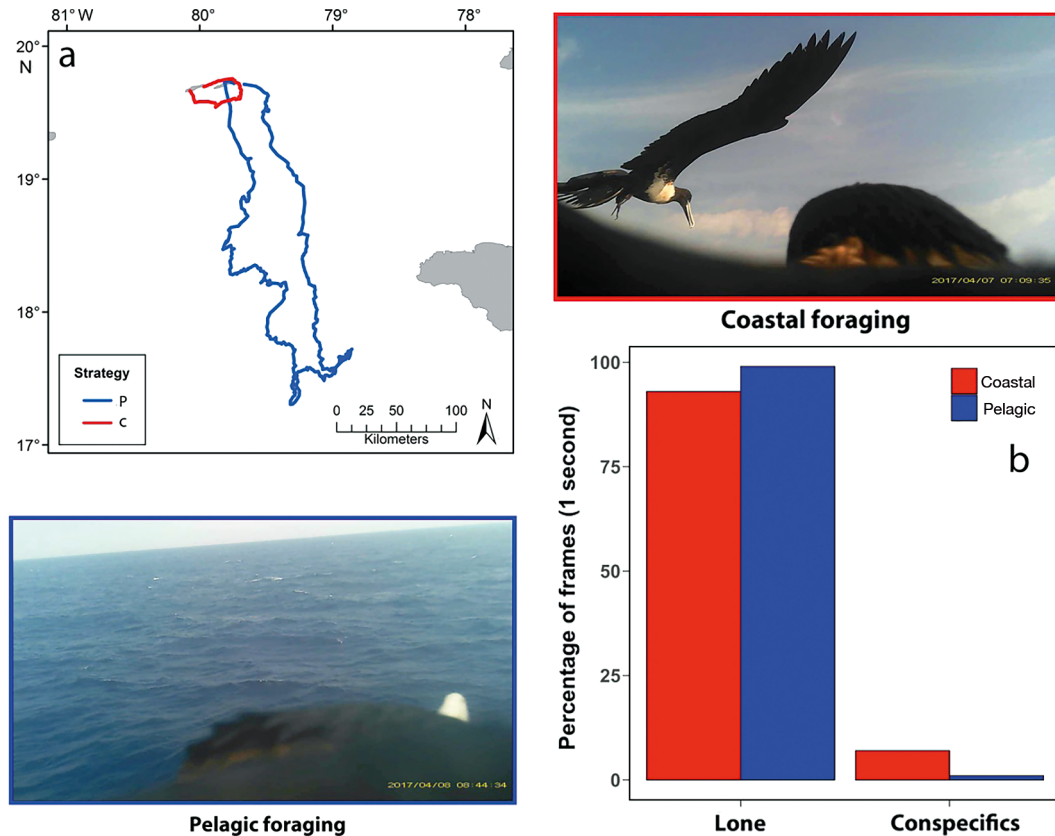


Fig. 5. (a) Foraging trips of a magnificent frigatebird tracked with video and GPS data loggers from Little Cayman, Cayman Islands, in April 2017, which engaged in both coastal (C, red) and pelagic (P, blue) foraging behaviours. (b) Proportion of video frames during coastal and pelagic movements during which the bird was observed alone or interacting with conspecifics

Coastal prey resources associated with static features such as fringing coral reefs probably represent more predictable foraging habitats than pelagic environments where frigatebirds target schooling fish that inhabit surface waters, such as flying fish and ballyhoo (Hazen et al. 2013). Furthermore, predictable opportunities for kleptoparasitism occur in coastal waters that are adjacent to breeding colonies of other seabirds (i.e. red-footed boobies, brown boobies and white-tailed tropicbirds on the Cayman Islands). The energy gain from food resources obtained in coastal and pelagic habitats is also likely to differ, which could influence required foraging and feeding rates (Ydenberg et al. 1994, Ydenberg 1994, Markman et al. 2004). The reason for the differential use of these habitats is unknown but it is interesting to note that, after being released from the constraints of central place foraging, failed breeders of both sexes foraged at distance from the colony in highly coastal waters that border other states and territories (Fig. S4), strategy also observed in other frigatebird populations (Hennicke et al. 2015).

Foraging flexibility may be associated with the trade-off between self-maintenance and offspring provisioning, with individuals alternating between these 2 forms of investment (McNamara & Houston 1997). No obvious cyclical pattern in coastal and pelagic strategies was found (Fig. S3), as might be expected with bimodal foragers that alternate between foraging trips for self-maintenance and chick-provisioning (e.g. Weimerskirch 1998, Garthe et al. 2003, Welcker et al. 2009a). Nevertheless, tropical species may be less likely to show strong periodicity in use of different strategies for these alternative purposes than temperate species in which alternating behaviours have been observed, and environmental factors (e.g. wind direction and speed) may instead play a role in influencing foraging behaviour (Weimerskirch et al. 2010, 2016). The nutritional requirements of adults and offspring often differ, and it may be that the food web targeted varies depending on whether adults are self-feeding or provisioning young (Murphy 1996, Markman et al. 2004). Nonetheless, if resources are more predictable in nearshore environments, which also require less travel time to access,

then there are likely to be other factors involved in driving individuals to engage in pelagic foraging.

Interspecific competition is likely to be higher close to colonies, where the available pool of resources can become locally depleted by the population (Ashmole 1971, Gaston et al. 2007). Observed variability in foraging strategy may thus be driven (or partially driven) by intense competition within productive nearshore environments adjacent to the colony (Oppel et al. 2015). In the case of magnificent frigatebirds, competition associated with size differences may be an underlying mechanism, with larger individuals (females) out-competing smaller individuals (males) in nearshore waters (Trefry & Diamond 2017 and references therein). Both the tracking and dietary data in the present study suggest that coastal foraging is important in this population, highlighted by the fact that adults commute to distant coastal areas to feed when actively provisioning chicks (in addition to after failing a breeding attempt). Pelagic foraging may thus be influenced by levels of competition in coastal areas during periods of central-place foraging, as longer foraging trips will result in lower feeding rates to chicks and, for some seabirds, can have higher energetic costs associated with travel, although this may not be an issue for frigatebirds due to their highly efficient flight (Chaurand & Weimerskirch 1994, Weimerskirch 1998). Preliminary video data provide support for the idea that competition may influence observed differences in at-sea behaviour within the tracked population: we found evidence for regular multi-species aggregations and conspecific interactions during coastal foraging in our recorded video footage which were not observed during pelagic foraging.

4.2. Sex-based differences in foraging behaviour and parental roles

Sex-based differences in feeding ecology in terms of dietary habits and kleptoparasitic behaviour are known amongst frigatebirds (Gilardi 1994, Megyesi & Griffin 1996, Le Corre & Jouventin 1997, Lagarde et al. 2001) and other tropical Suliformes (Weimerskirch et al. 2006a, 2009). In most cases (including at this study site, R. Austin et al. unpublished data), females are more likely to kleptoparasitise other species (Osorno et al. 1992), and this difference has again been predominantly attributed to size, with males thought to be competitively excluded, which may explain why males foraged on average further from the colony in our study. Sex-based differences

in morphology may also influence factors such as flight performance, that may in turn result in differences in movement behaviour. For example, smaller males may possess greater aerial agility than females (Jehl & Murray 1986, Trefry & Diamond 2017), and higher wing loadings in females may allow faster gliding flight (e.g. Shaffer et al. 2001, Phillips et al. 2004), which could drive different habitat preferences. Nevertheless, higher wing loadings might be expected to confer an advantage to female frigatebirds during offshore foraging, enabling them to travel further from the coast than males (Trefry & Diamond 2017), and this was not what we observed in our study.

It is also highly plausible that different parental roles observed between the sexes may be involved in shaping the observed behaviour. Female frigatebirds feed chicks more frequently and carry greater quantities of food than males during periods of biparental care (Calixto-Albarrán & Osorno 2000, Osorno & Székely 2004). Therefore, ties to the colony may be greater for females, who preferentially choose to minimise costs associated with commuting with a heavy food load during chick-provisioning trips (Cuthill & Kacelnik 1990). Males may therefore be freer to travel to profitable pelagic areas to forage. Alternatively, an interplay may exist between size-mediated competition and levels of parental investment (Lagarde et al. 2004, Osorno & Székely 2004).

No differences were found in trip characteristics between early and late chick-rearing stages, regardless of sex, consistent with existing suggestions that feeding rates are unrelated to the age of the chick in this species (Osorno & Székely 2004). Nevertheless, the majority of tags detached from birds prior to the main period of male desertion from nests (late May to June; Diamond 1972, R. Austin pers. obs.). Therefore, we are likely to have missed periods associated with sharp changes in levels of parental care, which would most likely further influence foraging behaviour. Females are known to substantially increase feeding rates of chicks once the male deserts the nest (Osorno & Székely 2004) and thus are more likely to alter their foraging behaviour in response to increased energetic demands during this period. Understanding how at-sea behaviour may change in response to the switch from biparental to uniparental care is therefore a priority for future work.

The patterns in foraging behaviour reported here highlight the vulnerability of magnificent frigatebirds to anthropogenic activity in coastal environments and are therefore relevant to conservation. Not only were nearshore areas around the Cayman

Islands important for chick-rearing individuals, but frigatebirds used highly coastal regions in several other states and territories, some of which are at considerable distances from their island home. This highlights the high potential for population mixing within the Caribbean region and indicates a need for trans-boundary cooperative management strategies to effectively conserve this species throughout its foraging range. The flexible nature of their foraging suggests that while this species may be at risk from pressures both in pelagic and coastal environments, populations may also have some capacity to buffer the effects of human disturbance. Alternatively, should birds employing one strategy be exposed to greater mortality risk than those using the other, sex biases in mortality could occur, with implications for population structure (e.g. Ryan & Boix-Hinzen 1999, Nel et al. 2002, Baker et al. 2007). In summary, magnificent frigatebirds engage in bimodal patterns of foraging, and are reliant on prey resources in coastal areas that experience high levels of human activity, highlighting the need for effective management strategies for this wide-ranging species throughout its distribution range.

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