



Giambalvo, G., Y. V. Albores-Barajas, C. Soldatini, M. P. Rosas Hernandez, and N. C. Rattenborg. 2022. Environmental drivers of sex-biased foraging behavior in Magnificent Frigatebird in Baja California Sur, Mexico. *Avian Conservation and Ecology* 17(2):25. <https://doi.org/10.5751/ACE-02202-170225>

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Research Paper

Environmental drivers of sex-biased foraging behavior in Magnificent Frigatebird in Baja California Sur, Mexico

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ABSTRACT. Understanding the characteristics of a species's distribution represents a challenge in marine environments because movement patterns and foraging areas are restricted by highly dynamic spatiotemporal variations in environmental conditions. In response to this heterogeneous context, marine predators such as seabirds need to maximize their foraging efficiency, especially during the breeding season, when movement is restricted by the need to return to the nest. Biologging technologies such as satellite transmitters and Global Positioning System (GPS) receivers allow researchers to track birds at sea and investigate the relationship between foraging strategy and changing oceanographic features. Our study focuses on characterizing the feeding areas of Magnificent Frigatebird (*Fregata magnificens*) breeding in Baja California Sur, Mexico. We used GPS receivers to track the foraging flights of frigatebirds during 2017–2019, identifying the core foraging areas and characterizing environmental conditions and marine productivity in these areas. Individuals repeatedly selected areas close to the colonies located in Espíritu Santo archipelago (Gulf of California) and Santa Margarita Island (Pacific Ocean). However, some males flew to more distant and equally productive areas to the south and north of the Baja California peninsula. We presume that the differential use of foraging areas between males and females reflects biometrical and behavioral differences of the sexes, which may explain the relationships between foraging behavior and breeding, intraspecific competition, and sex-based differences in parental investment. Because frigatebirds are considered indicators of marine environmental conditions, our data are useful to identify areas where prey species aggregate in space and time and, therefore, to expand the boundaries of existing marine protected areas. Data on seabird foraging ranges described here can be useful for delineating marine protected area boundaries and can be considered suitable candidates for inclusion in appropriately designated regional marine spatial planning.

Facteurs environnementaux sous-jacents aux stratégies d'alimentation différentes selon le sexe chez la Frégate superbe en Basse-Californie du Sud, Mexique

RÉSUMÉ. La compréhension des caractéristiques de la répartition d'une espèce représente un défi dans les environnements marins, car les habitudes de déplacement et les zones d'alimentation sont limitées par des variations spatio-temporelles hautement dynamiques des conditions environnementales. En réaction à ce contexte hétérogène, les prédateurs marins tels que les oiseaux de mer doivent maximiser l'efficacité de leur recherche de nourriture, en particulier pendant la saison de reproduction, alors que les déplacements sont limités par la nécessité de retourner au nid. Les technologies captant des indices biologiques, telles que les émetteurs satellitaires et les récepteurs GPS (Global Positioning System), permettent aux chercheurs de suivre les oiseaux en mer et d'étudier la relation entre la stratégie d'alimentation et les caractéristiques océanographiques changeantes. Notre étude porte sur la caractérisation des zones d'alimentation de la Frégate superbe (*Fregata magnificens*) nichant en Basse-Californie du Sud, au Mexique. Nous avons utilisé des récepteurs GPS pour suivre les vols des frégates en quête de nourriture pendant la période 2017-2019, et avons identifié les zones principales d'alimentation ainsi que caractérisé les conditions environnementales et la productivité marine dans ces zones. Les individus ont choisi à plusieurs reprises des zones proches des colonies situées dans l'archipel d'Espíritu Santo (golfe de Californie) et sur l'île de Santa Margarita (océan Pacifique). Cependant, certains mâles ont volé vers des zones plus éloignées et tout aussi productives au sud et au nord de la péninsule de Basse-Californie. Nous croyons que l'utilisation de zones d'alimentation différentes entre les mâles et les femelles reflète des différences biométriques et comportementales entre les sexes, ce qui pourrait expliquer les relations entre l'alimentation et la reproduction, la compétition intraspécifique et les différences entre les sexes dans l'investissement parental. Les frégates étant considérées comme des indicateurs des conditions environnementales marines, nos données sont utiles pour qu'on puisse identifier les zones où les espèces proies se regroupent dans l'espace et le temps et, par conséquent, qu'on puisse étendre les limites des zones marines protégées existantes. Les données sur les aires d'alimentation d'oiseaux de mer décrites ici peuvent servir à la délimitation des aires marines protégées et peuvent être considérées comme aires candidates à inclure dans la planification spatiale marine régionale.

Key Words: *environmental characteristics; foraging movements; GPS receivers; habitat use*

INTRODUCTION

Low productivity of tropical oceanic waters imposes restrictions on tropical predators, including seabirds, inducing the evolution of appropriate foraging strategies (Ainley and Boekelheide 1983). In the tropics, phytoplankton production is limited, and the total biomass at subsequent trophic levels is similarly affected, causing strong selective pressure on foraging strategies in tropical seabirds (Ballance and Pitman 1999). In addition, these environmental conditions can also affect life history traits such as low fecundity and high adult survival (Schreiber and Burger 2001). Frigatebirds are probably extreme examples of such evolution (Weimerskirch et al. 2004). They are long-lived seabirds inhabiting tropical environments and have extremely efficient flight in terms of morphological adaptations and low energetic costs (Ballance and Pitman 1999). They are oceanic predators that never land on the sea surface, maintaining flight for days to months (Weimerskirch et al. 2003, 2004, 2016); as shown in Great Frigatebirds (*Fregata minor*), they can also sleep in flight (Rattenborg et al. 2016). Because of their particular morphology and flight ability, it has been suggested that these seabirds have evolved specific flight strategies (Weimerskirch et al. 2003) associated with the trade-off between self-maintenance and offspring provisioning, with individuals alternating between these two forms of investment during the breeding season (Austin et al. 2019). Frigatebirds show dramatically different levels of parental investment: males and females share duties equally during incubation (Hennicke et al. 2015), but males desert the colony when the chick is three to four months old and leave females to complete the raising of the young for more than nine months after fledging (Diamond 1972, Osorno-Cepeda 1996). This strong sex difference in parental care makes them interesting candidates for investigating foraging strategies because these species might also be expected to show divergence in their at-sea behavior, a potential source of interindividual variability in movement behavior. When constrained during the breeding season by the requirement of central-place foraging, individuals share similar feeding locations and spatial convergence in foraging strategy (Phillips et al. 2007). However, between-sex differences in foraging area selection are evident during the nonbreeding season, reducing resource overlap (Mott et al. 2017), probably to minimize intraspecific competition for prey and maximize individual reproductive success (Hennicke et al. 2015, Austin et al. 2019). Many studies have investigated the foraging strategy of frigatebirds, revealing that foraging habitats are primarily oceanic for the Great Frigatebird and Christmas Island Frigatebird (*F. andrewsi*; Hennicke et al. 2015), whereas the Magnificent Frigatebird (*F. magnificens*) exhibits bimodal and sex-based foraging strategies (Hennicke et al. 2015), engaging in both coastal and pelagic movements (Austin et al. 2019).

Marine productivity is an important factor for frigatebirds in selecting foraging areas (Weimerskirch et al. 2004) and structuring their distribution at sea. The environment in which they live forces frigatebirds to apply plastic strategies to take advantage of the unpredictable and patchy prey distribution of tropical waters, and sex-differential foraging behavior may be one of the strategies for coping with changing environmental conditions. Most of the available information about foraging strategy is concentrated on Great Frigatebirds that forage at great distances from their breeding grounds, similar to large seabirds such as albatrosses, who are able to move at much greater speeds (Weimerskirch et al.

2004). In contrast, Magnificent Frigatebirds have been observed remaining close to the breeding grounds (Weimerskirch et al. 2003), foraging in coastal waters, often in the relative vicinity of their breeding colonies (Diamond and Schreiber 2002, Weimerskirch et al. 2006).

Magnificent Frigatebirds nest on islands throughout the Caribbean and in tropical areas of both coasts of Central and South America (Diamond and Schreiber 2002), from Florida to Ecuador (including the Galapagos), south Brazil, and off the coast of Africa (BirdLife International 2020, 2022). Despite their large range, there is a lack of detailed information on the sex-based distribution and environmental characteristics that drive Magnificent Frigatebirds' choice of foraging areas around the peninsula of Baja California, where two important colonies are located (Diamond 1973) and where seabird populations have been experiencing dramatic changes in the last decades due to threats in both terrestrial and marine habitats (Lewison et al. 2012). In most areas where information is available, populations of Magnificent Frigatebird are declining, apparently due to loss of habitat, disturbance, and tourist and urban development (Diamond and Schreiber 2002). Mangrove cover loss, reduction of food availability due to an increase in fishing of small pelagic fish on the west coast of Baja California Sur, and elevated concentrations of trace elements in Magnificent Frigatebirds' food supply may have caused a population decline (Marrón et al. 2021). It is estimated that > 18,000 pairs have been lost from the colonies of Baja California Sur (Moreno and Carmona 1988, Diamond and Schreiber 2002, Marrón et al. 2014). The Magnificent Frigatebird population decline is particularly steep in the Estero Las Tijeras, the species' main nesting area in the Magdalena lagoon complex. At this site, 20,117 pairs were reported in 1986–1987 (Moreno and Carmona 1988), but in the last 15 years, alarming changes occurred in the number of individuals, decreasing from 16,767 pairs in 2002–2003 (Zárate-Ovando et al. 2006) to only 532 in 2015 (Marrón et al. 2021), and only one nest in 2017 (Albores-Barajas and Soldatini, *personal observation*). In the same year at San Gabriel Bay, in the Espíritu Santo Archipelago, 912 nesting pairs were counted. Although two new breeding colonies were found in the Santo Domingo channel, with 90 and 36 pairs, respectively, to date, the Espíritu Santo Archipelago supports and hosts the largest number of Magnificent Frigatebirds in Baja California Sur (Marrón et al. 2021).

Despite the recently detected population decrease, the species is not under protection in the Official Mexican Standard for the Environmental Protection of Mexican Endangered Native Species (NOM-059) and is considered Least Concern in the International Union for Conservation of Nature Red List (Government of Mexico 2010). It is therefore essential to obtain more information to better define the state of conservation of Magnificent Frigatebirds. Moreover, understanding the foraging strategies of tropical seabirds is important (Ricklefs 1990), given their role as biological indicators of ecosystem condition (Weimerskirch et al. 2004). However, most studies have been carried out in polar and temperate areas (Ballance and Pitman 1999) and have collected short-term data, only including observations made within the same season or for two to four years but centered on the breeding seasons (Watanuki 1992, Bolnick et al. 2003, Bell et al. 2009, Ceia and Ramos 2015, Phillips et al. 2017).

Using a novel approach of year-round Global Positioning System (GPS) tracking survey, we investigated Magnificent Frigatebird sex-specific foraging movements and habitat use for the population nesting in the Espíritu Santo Archipelago and Santa Margarita Island (Mexico) colonies, from the chick-rearing stage in 2017 to the post-reproduction stage in 2019. Sex-based differences in reproductive investment and physiology can result in an interesting variability in foraging behavior (Austin et al. 2019). Especially in frigatebirds, the extreme sex differences in parental roles might also be expected to show variance in at-sea behavior and in habitat use. We described four oceanographic features of the foraging areas: sea surface temperature (SST), chlorophyll a concentration ([CHLa]), bathymetry (BAT), and particulate organic carbon (POC). These variables are often considered in quantitative analyses to evaluate seabird distributions at sea (Ainley et al. 2005, Ballance 2007, Grémillet et al. 2008, Soldatini et al. 2019), and the abundance of seabirds is highly correlated with indices of ocean productivity (Ainley et al. 2005). High values of CHLa, low SST, and shallower depth dictate higher productivity patterns (Longhurst 1998) and, consequently, an enhanced concentration of prey and predators (Hyrenbach et al. 2007). Because frigatebirds are apex predators feeding at the top of the food chain, physical features or combinations of oceanic parameters represent a proxy for prey abundance or availability (Ballance et al. 2006). Thus, the oceanographic variables examined here are some of those shown to have a major effect on seabird distributions at sea (Ainley et al. 2005).

We aimed to examine whether males and females exhibited different movement parameters and to compare environmental characteristics of the feeding areas during the three years of data collection. The results will contribute to developing and improving regional marine spatial planning to expand or to establish priority conservation areas in the main Mexican colonies of the species, which is highly consequential for its conservation.

METHODS

Study sites

Espíritu Santo archipelago

The Espíritu Santo archipelago is located to the east of the Bay of La Paz, on the southeast coast of the Baja California peninsula (24.52°, -110.33°). The archipelago comprises several smaller islands and is included in the “*Islas del Golfo de California*” Flora and Fauna Protection Area (Government of Mexico 2002). The climate is hot and dry, with an average annual rainfall of 180 mm, concentrated in summer (Ortega-Rubio et al. 2019). The most important Magnificent Frigatebird colony of the Baja California Peninsula is located at San Gabriel Bay (24.48°, -110.35°) on the southwest side of the archipelago, in the Gulf of California. Nests are built on red mangrove (*Rhizophora mangle*) growing on 297 m of isolated rocks that are difficult to reach by terrestrial predators due to two channels blocking their access.

Santa Margarita Island

The Santa Margarita colony is located on the southern tip of Santa Margarita Island (24.44°, -111.83°) and is part of the insular complex of Magdalena Lagoon, on the Pacific coast of Baja California Sur. The climate is hot semi-arid, with an annual

rainfall that fluctuates between 48 and 153 mm and, consequently, the lagoon complex does not receive freshwater most of the year (Funes-Rodríguez et al. 1998). At the southeast end of the island is a mangrove swamp consisting of three species of mangrove: *Rhizophora mangle*, black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*; Amador et al. 2006). The latter is used by Magnificent Frigatebirds for both nesting and perching (Moreno and Carmona 1988).

Data collection

In April 2017, 20 adult Magnificent Frigatebirds were captured and tagged with Gipsy Remote System Solar-powered GPS receivers (Technosmart Europa, Roma, Italy), equipped with pressure, temperature, and acceleration sensors set to record data every 10 min. The GPS locations were not interpolated. The total weight of the device is 38 g (2–3% of adult body mass), similar to tags used in other frigatebird studies (Weimerskirch et al. 2006, 2010). Data were downloaded to antennas placed in each colony. Because of difficulties in recapturing birds, these loggers were not retrieved, and when they ceased transmitting, they were assumed to have been lost.

Of the 20 tagged individuals, five males and five females were caught in the Espíritu Santo colony and four males and six females on Santa Margarita Island. Of the 11 females, 5 had a chick in the nest where they were captured, so we can assume that these 5 females were reproductive, meaning that they would be engaged in chick-rearing and post-fledging care for the subsequent year. Birds were captured at their nests or roosting sites by hand at night and brought outside the colony to avoid additional disturbance. We deployed the GPS receivers using a leg harness made of Teflon. The sex of the birds was determined by plumage: males are entirely black, whereas females are blackish-brown, except for a prominent white patch across the breast. After animal handling, birds were released at the edge of the colony (within 50 m of their nests), and they returned to their nests within 5 min. The total time from catch to release was approximately 7 min. All fieldwork and animal handling were performed in accordance with the principles and guidelines of laws on animal welfare and under permission numbers SGPA/DGVS/00321/16 and SGPA/DGVS/00404/17 from the Direction of Wildlife in Mexico (*Dirección General de Vida Silvestre*) of the Ministry of the Environment and Natural Resources (*Secretaría de Medio Ambiente y Recursos Naturales*, or SEMARNAT).

Based on the species' biology (Carmona et al. 1995, Diamond and Schreiber 2002), we partitioned years into four seasons: chick rearing (April to June), late chick rearing (July to September), and pre-breeding (October to December) in 2017; and reproduction (January to March), chick rearing, late chick rearing, and pre-breeding in 2018 and 2019. Females breed only in alternate years (Diamond and Schreiber 2002), so at any given season, females might be in different stages.

Data analysis

To investigate differences in foraging patterns (trip duration, maximum distance from colony, distance traveled) between sexes and years, we compiled a complete database containing GPS device identity (device.ID), time (day, month, year, and hour), speed, altitude, and geographic coordinates. From these data, it was possible to calculate movement parameters such as distance

traveled, foraging duration, and trip distance for each individual and foraging area.

All statistical analyses were conducted in R 4.0.2 (R Core Team 2019). Tracking data were classified by applying expectation-maximization binary clustering (Garriga et al. 2016). This method groups data using speeds (calculated as a ratio between time and distance traveled obtained by GPS points) and turns, which allows the identification of foraging behaviors: low speeds and high numbers of turns were associated with intensive search behavior for food, whereas high speeds and high numbers of turns were interpreted as an extensive search (Garriga et al. 2016). All the points were examined for altitude, confirming that the foraging events occur largely below 50 m of altitude.

Movement parameters

We used Kendall's τ -b correlation test (R Core Team 2019) to examine correlations between trip duration, trip distance, and foraging trip duration to avoid using correlated variables in the same model. We used the Kruskal-Wallis test to examine the differences in distance traveled between sexes, years, and seasons because the data were not normally distributed. We applied two generalized linear mixed models (GLMMs) to investigate the influence of sex, year, and season on average distance traveled and on trip duration. All GLMMs included bird identity as a random term to account for pseudoreplication.

Environmental variables

We considered four environmental variables: BAT, [CHL_a], SST, and POC. Only GPS points related to at-sea behavior were included in the analysis by applying a filter on bathymetry to exclude data on land. The BAT (in m) data were downloaded from the "etopo360" data set, with 0.017° built with horizontal data (WSG-84) and vertical data (mean sea level). The [CHL_a] (in mg/m³) data were downloaded from the "erdVHNchlamday" data set, with a resolution of 750 m taken by VIIRS (Visible Infrared Imaging Radiometer Suite) sensors from the Suomi_NPP satellite. The SST (in °C) data at 1 × 1 km resolution were obtained from the Group for High Resolution Sea Surface Temperature - Multiscale Ultra-high Resolution (GHRSSST-MUR) from the "jplMURSST41mday" data set. The POC (in mg/m³) at L3 4 × 4 km resolution were downloaded from the "erdVH2018pocmday" data set taken by VIIRS. The monthly average value for each variable was downloaded for every season of 2017–2019, and a complete data set was elaborated using the "rerdapXtracto" package in R (Mendelssohn 2019). To estimate the areas mainly used for foraging, we used kernel density estimation set to 75% using the KDE function from the package "ks" (Duong 2007). The kernel 50% is usually considered the most appropriate percentage representing the home range of foraging animals, although some analyses suggest that values around 70% can be more appropriate for many seabirds who tend to travel much further during incubation (BirdLife International 2009, Lascelles et al. 2016, Dias et al. 2018). Moreover, as the range of frigatebirds is very wide, the 95% kernel density estimation would not have allowed the delineation of polygons for the environmental analysis but would have generated isolated points because it is difficult for many individuals to coincide in the same point. The core areas used by the individuals were then identified as polygons that were subsequently used as references to obtain the environmental data from the ERDDAP server of the National Oceanic and Atmospheric Administration to evaluate the

characteristics of the sites used by individuals and identify their oceanographic features.

To test for differences in environmental conditions of foraging areas between years, seasons, and sexes, we used GLMM models with the mean of each environmental variable as the response variable; year, season, and sex as predictor variables; and individual as a random effect. We tested for correlations between average values of [CHL_a], SST, BAT, and POC prior to all analyses using Spearman's rank correlation tests, and correlated variables were precluded from appearing in the same tests and models. We applied a Kruskal-Wallis test to examine the differences in foraging area selection between years, seasons, and sexes. A pairwise *t*-test with Bonferroni correction was applied as a post-hoc test to perform all possible pairwise comparisons. For all tests, significance (α) was set at 0.05. Data are summarized as mean \pm standard error (SE), with minimum and maximum values for the study seasons. Akaike Information Criterion (AIC) weights were used for model ranking and selection (Akaike 1973, Burnham and Anderson 2002).

RESULTS

We obtained 878,566 GPS fixes; of these, 260,863 represent foraging points (45,691, 22,210, and 18,831 for males, and 56,819, 76,329, and 40,983 for females, in 2017, 2018, and 2019, respectively). From the foraging points, we extracted 1227 complete trips during the three years of study. Start and end times of foraging trips were determined from locational data by considering the time between the last fix on the nest before leaving the colony and last fix at sea before returning to the nest. In 2017, we obtained 362 trips from 10 females and 41 trips from 9 males. During 2018, we obtained 351 trips from 10 females and 105 trips from 6 males. In 2019, we obtained 309 trips from 7 females and 59 trips from 4 males.

Movement parameters

We found a significant difference in distance traveled between sexes ($\chi^2 = 23.15$, $P < 0.01$, $df = 1$), years ($\chi^2 = 29.102$, $P < 0.01$, $df = 2$), and seasons ($\chi^2 = 58.705$, $P < 0.01$, $df = 3$). We found a positive relationship between all parameters: longer trips took more time to complete, and, during those longer trips, individuals spent more time foraging (trip duration and trip distance, $\tau = 0.665$, $P < 0.001$; foraging duration and trip distance, $\tau = 0.613$, $P < 0.001$; trip duration and foraging duration, $\tau = 0.814$, $P < 0.001$). Males showed higher values in all movement parameters during each season compared to females (Table 1). The maximum distance traveled was recorded during the chick-rearing period, with an average of 1309.26 ± 328.95 km for males and 325.61 ± 46.59 km for females. The longest trip was done by a male: it flew 23,312.27 km during 150 days from 07 May to 10 October 2017. The timing corresponds with the late chick-rearing period when males abandon the colony in early summer and return for the next breeding season in autumn. We used AIC model selection to distinguish among a set of possible models describing the relationship between year, season, and sex on distance traveled. The best-fitting model, carrying 80% of the cumulative model weight (AIC = 60,150, Table 2), includes sex and season, with an interaction effect. Males and females travel different distances depending on the seasons, especially during the chick-rearing stage (Fig. 1), when distance traveled increased in both sexes. This pattern remained constant throughout the years of study.

Fig. 1. Maps of Baja California Sur showing Magnificent Frigatebird foraging movements during the beginning of chick-rearing period (April 2017). Lines indicate foraging tracks of frigatebirds determined by Global Positioning System receivers; star = colony location. Left panel (blue lines) are males; right panel (orange lines) are females.

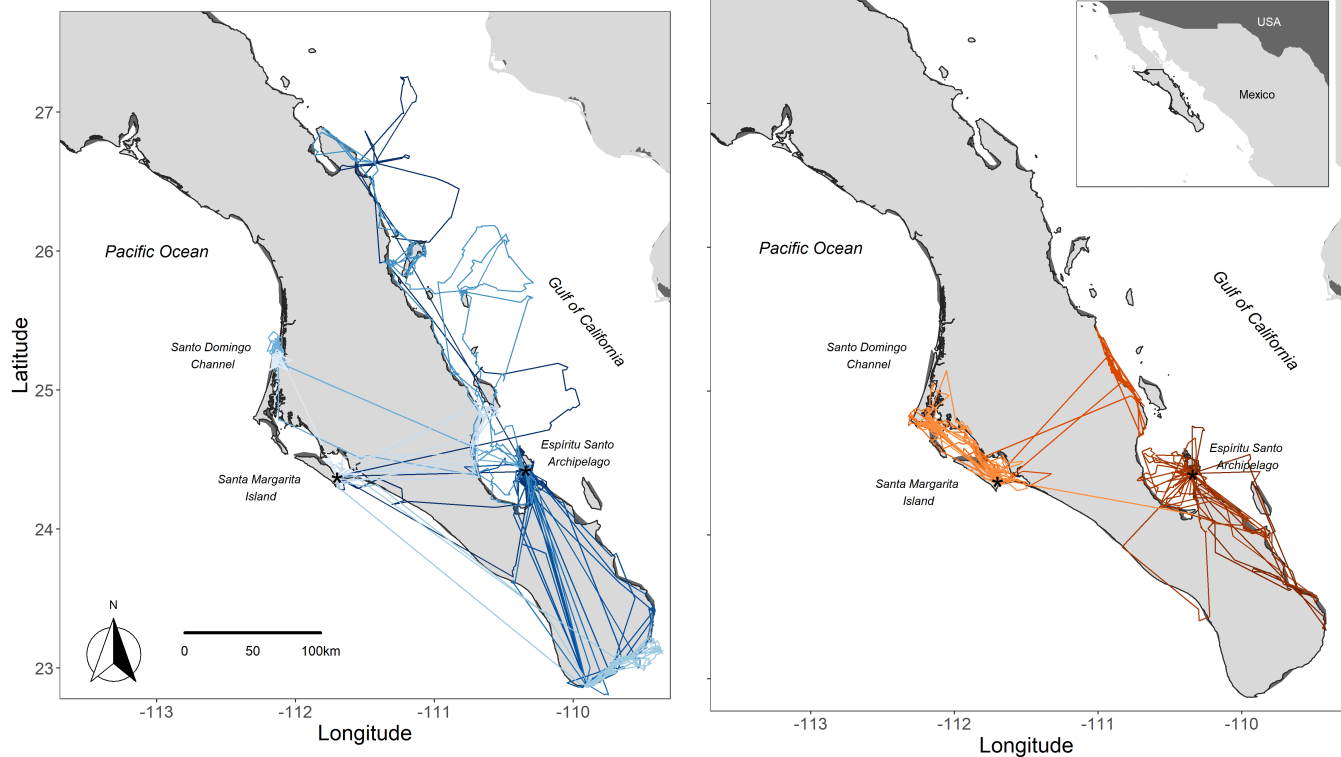


Table 1. Summary of female and male Magnificent Frigatebird movement and foraging parameters in different seasons.

Season	Parameter	Female (mean ± SE)	Male (mean ± SE)
Chick rearing	Distance traveled (km)	215.68 ± 8.25	399.96 ± 50.71
	Trip duration (h)	20.90 ± 1.17	50.39 ± 7.62
	Foraging trip duration (h)	14.43 ± 0.90	34.06 ± 5.33
Late chick rearing	Distance traveled (km)	175.83 ± 6.73	359.41 ± 82.57
	Trip duration (h)	16.65 ± 0.99	55.25 ± 12.35
	Foraging trip duration (h)	10.76 ± 0.69	37.52 ± 9.11
Pre-breeding	Distance traveled (km)	167.00 ± 6.79	224.04 ± 40.47
	Trip duration (h)	17.22 ± 1.26	45.97 ± 10.06
	Foraging trip duration (h)	11.47 ± 0.98	30.60 ± 7.70
Reproduction	Distance traveled (km)	288.12 ± 19.28	540.75 ± 93.29
	Trip duration (h)	34.32 ± 2.80	87.50 ± 14.77
	Foraging trip duration (h)	23.68 ± 2.19	56.57 ± 10.33

Environmental variables

Using kernel density estimation to 75%, we identified 27 polygons for females (9 in 2017, 8 in 2018, 10 in 2019) and 23 for males (7, 7, and 9 in 2017, 2018, and 2019, respectively). We obtained the corresponding environmental variables from these areas. The environmental characteristics of the foraging areas differed between the sexes (Table 3). The maximum [CHLa] recorded in the areas selected by males corresponded to the late chick-rearing

Table 2. Generalized linear mixed model results ranked by Akaike Information Criterion (AIC) values for distance traveled by male and female Magnificent Frigatebirds during the study period. Only the best-performing models based on AIC values are reported. Bird identity was included as random factor to account for pseudoreplication. Δ AIC = difference in AIC score between the best model and the model being compared; K = number of parameters in the model; wAIC = AIC weight, which is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed.

Model	AIC	Δ AIC	K	wAIC	Log-likelihood
distance = sex × season	60,150	0	9	0.80	-30,066.24
distance = sex × season + year	60,153	3	11	0.19	-30,065.68
distance = sex + season	60,171	21	6	0	-30,079.65
distance = sex	60,180	30	3	0	-30,087.23
distance = sex + year	60,183	33	5	0	-30,086.64
distance = year	60,235	85	4	0	-300,113.26

period in 2017 (16.2 mg/m³). For females, the maximum [CHLa] was 13.86 mg/m³ during the chick-rearing period in 2019. Mean values of [CHLa] show significant differences between areas used by males and females ($\chi^2 = 8.8246$, $P = 0.003$), indicating that

Table 3. Values of environmental characteristics by Magnificent Frigatebird sex and season (mean ± standard error). [CHLa] = sea surface chlorophyll a concentration, SST = sea surface temperature, BAT = bathymetry, POC = particulate organic carbon.

Sex	Season	[CHLa] (mg/m ³)	SST (°C)	BAT (m)	POC (mg/m ³)
Female	Chick rearing	6.66 ± 1.18	20.20 ± 0.906	-2.42 ± 0.410	228.0 ± 32.8
	Late chick rearing	2.36 ± 0.502	27.50 ± 0.502	-9.01 ± 3.79	195.0 ± 17.9
	Pre-breeding	2.77 ± 0.515	25.20 ± 0.524	-21.6 ± 3.35	345.0 ± 85.6
	Reproduction	3.45 ± 0.532	20.40 ± 0.361	-8.47 ± 2.38	241.0 ± 31.3
Male	Chick rearing	8.31 ± 3.21	21.60 ± 0.594	-334.0 ± 85.9	109.0 ± 6.95
	Late chick rearing	9.48 ± 2.76	28.20 ± 0.521	-103.0 ± 50.3	268.0 ± 91.8
	Pre-breeding	4.39	26.40 ± 0.892	-63.60 ± 20.7	335.0 ± 68.3
	Reproduction	n/a	23.0 ± 0.347	-542.0 ± 16.6	91.80 ± 16.7

males select sites with higher productivity and enhanced prey concentrations. The mean SST of foraging areas was significantly different among seasons and years ($\chi^2 = 68.353$, $P < 0.01$ and $\chi^2 = 7.825$, $P = 0.01$, respectively), with lower temperatures of $18.11 \pm 0.67^\circ\text{C}$ (SD) during the chick-rearing season in 2018 for males and $18 \pm 0.62^\circ\text{C}$ (SD) during the chick-rearing season in 2019. Values of POC were different among years ($\chi^2 = 11.044$, $P = 0.004$), with a maximum of 364.6 mg/m^3 in 2017, 313.4 mg/m^3 in 2018, and 452.33 mg/m^3 in 2019. The average depth where foraging was recorded varied significantly between males and females ($\chi^2 = 12.632$, $P \leq 0.001$), among seasons ($\chi^2 = 15.962$, $P = 0.001$), and across years ($\chi^2 = 13.832$, $P = 0.001$). *T*-tests with Bonferroni correction as post-hoc analyses indicate a significant difference between the bathymetry of areas used by males and females ($P \leq 0.001$), showing that males made more offshore trips, reaching regions with -782.77 m in depth, whereas females remained close to the coast, preferring shallower areas with an average depth of -34 m . Moreover, adults changed foraging areas depending on the season, with a preference for feeding sites located in deeper areas during the late chick-rearing and reproduction periods (*t*-test with Bonferroni correction, $P = 0.034$).

The four variables considered, i.e., SST, [CHLa], BAT, and POC, were correlated (Table 4), so we compared models with these variables separately (Table 5). Foraging site selection was best explained by POC (AIC values: POC = 153.69, [CHLa] = 166.35, SST = 189.91, BAT = 196.84). The best model accounted for variability in POC and BAT between season and sexes as interactive effects.

Table 4. Spearman's rank correlation results for environmental characteristics of Magnificent Frigatebird foraging areas. [CHLa] = chlorophyll a concentration, SST = sea surface temperature, BAT = bathymetry, POC = particulate organic carbon.

Parameter	[CHLa]	SST	BAT	POC
[CHLa]	—	-0.57	0.11	0.66
SST	—	—	0.38	-0.49
BAT	—	—	—	-0.18
POC	—	—	—	—

Males and females exhibited sexual segregation for resources outside of the reproductive period but converged in the same feeding areas close to the colony during spring and early summer (Fig. 1). The main foraging areas along the peninsula used by females were concentrated in coastal areas near the Espiritu Santo

Table 5. Generalized linear mixed model results ranked by Akaike Information Criterion (AIC) values for drivers differentiating the choice of foraging area for male and female Magnificent Frigatebirds during the study period. Only the best-performing models based on AIC values are reported. ΔAIC = difference in AIC score between the best model and the model being compared; K = number of parameters in the model; wAIC = AIC weight, which is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed.

Model	AIC	ΔAIC	K	wAIC	Log-likelihood
area = season × sex × POC × BAT	68.82		33	1	-1.41
area = season × sex × [CHLa] × BAT	88.52	19.70	24	0	-20.26
area = sex × year × [CHLa] × BAT	94.99	26.17	17	0	-30.49
area = sex × [CHLa] + BAT	96.82	28.00	6	0	-42.41
area = year × [CHLa] × BAT	97.76	28.93	9	0	-39.88
area = season × sex × SST × BAT	108.68	39.86	31	0	-23.34
area = season + SST + BAT	144.26	75.44	7	0	-65.13

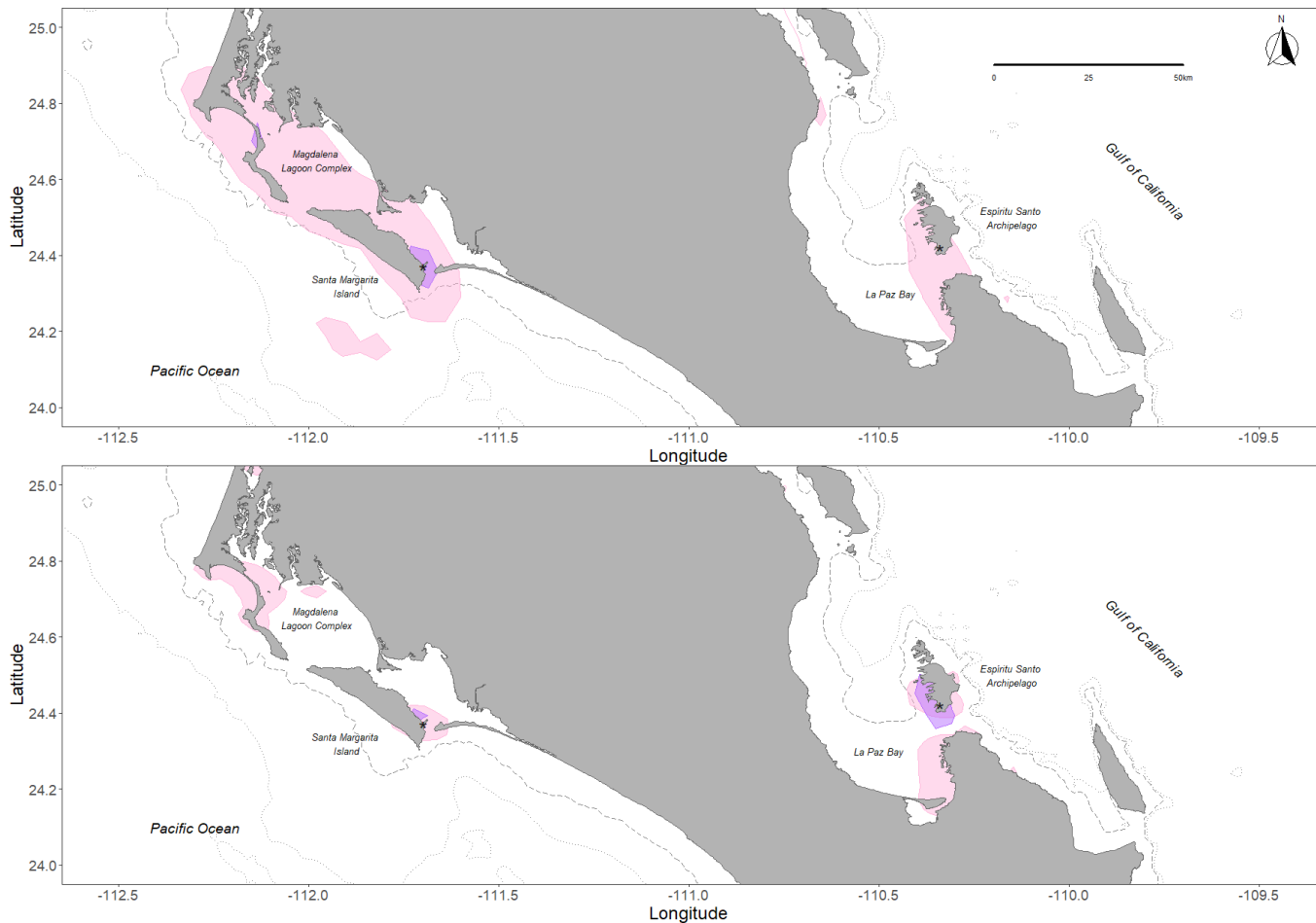
archipelago colony and Santa Margarita Island (Fig. 2). Males selected foraging sites to the north and south of the peninsula (Fig. 3). Both males and females were consistent in their choice of foraging areas throughout the study.

DISCUSSION

Our study shows substantial differences in habitat selection and use between the sexes of Magnificent Frigatebirds. We collected data on sex-specific foraging movements and habitat use over three years continuously, including reproduction, chick rearing, late chick rearing, and pre-breeding. Magnificent Frigatebirds are capable of traveling long distances (Diamond and Schreiber 2002), and males roam significantly further from the nest and coastline, traveling total distances and engaging in longer trips than females (Austin et al. 2019). We observed interseason variability in the choice of foraging areas and identified the environmental variables that drive this choice in individuals nesting in the main Mexican Pacific colonies.

Oceanographic features and marine productivity play an important role in the choice of Magnificent Frigatebird foraging destinations, revealing a seasonal pattern maintained during the three years of data collection. Seabird abundances are highly correlated with indices of ocean productivity (Ainley et al. 2005). For most seabirds, the main feeding areas are either relatively

Fig. 2. Maps of Baja California Sur showing Magnificent Frigatebird core foraging areas of females in 2017 (top panel) and 2018 (bottom panel). Pink polygons = 25% use distribution, purple polygons = 75% use distribution, dashed line = 100 m depth, dotted line = 250 m depth.

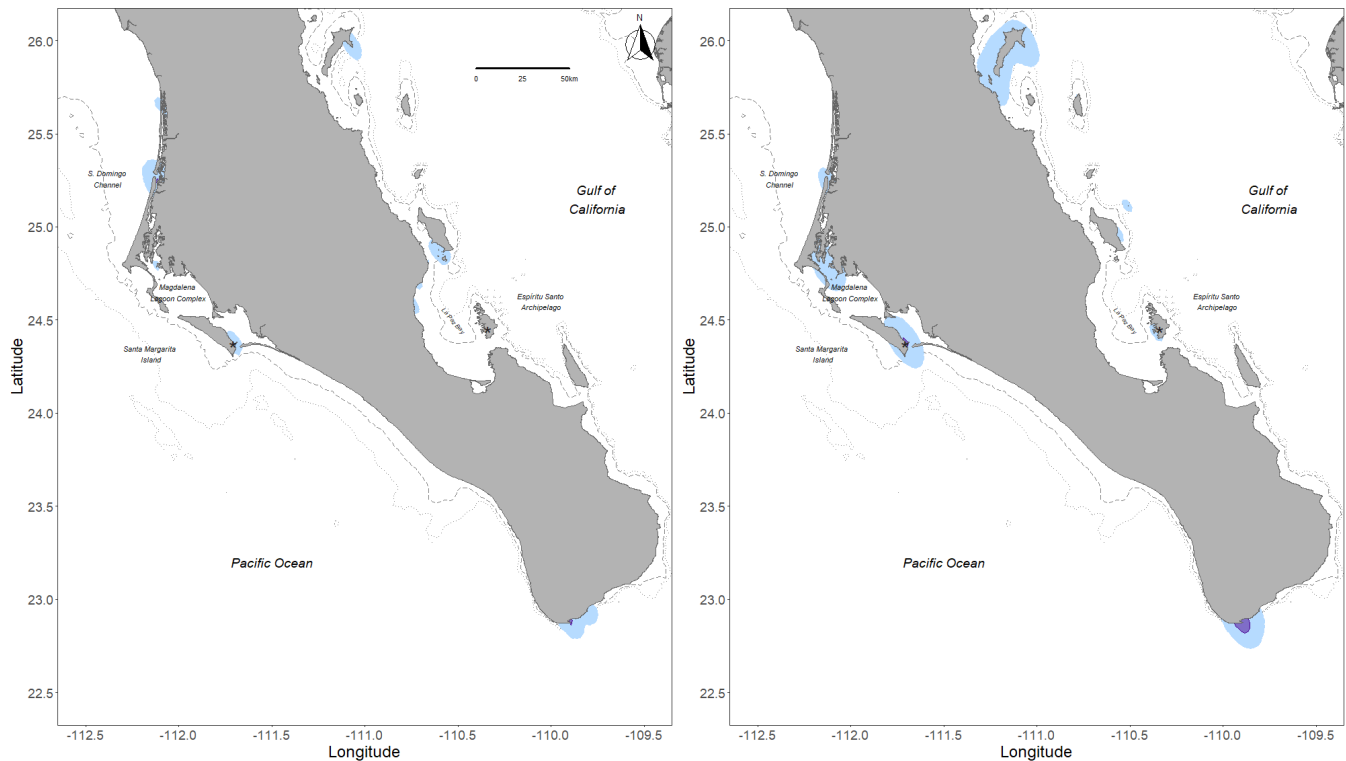


static (e.g., around sandbanks; Lascelles et al. 2012) or linked to dynamic processes and variables (Kappes et al. 2010, Žydelis et al. 2011) that enhance productivity and food availability. Such features include shelf breaks and seamounts (Thompson 2007), benthic habitats (Velando et al. 2005), gyres and eddies (Hyrenbach et al. 2006), frontal regions, convergence zones, and tidal currents (Ladd et al. 2005). In contrast to terrestrial landscapes, where habitat extensions are often better identified and documented, there are intrinsic difficulties in defining boundaries in dynamic and apparently featureless seascapes (Hyrenbach et al. 2000). Although marine protected areas might be made wide enough to accommodate this variability, the preferred choice of managers and legislators remains the protection of static sites. However, this strategy is highly prejudicial to the requirements of most pelagic marine species, including seabirds (Lascelles et al. 2012). A good foraging strategy for seabirds is simply to locate certain features such as physical gradients, including boundaries between currents, eddies, and water masses, that can concentrate nutrients and therefore enhance primary production (Ballance and Pitman 1999). Thus, the delineation of marine protected area boundaries may be

refined using information on seabird foraging ranges, considering such dynamic areas as suitable candidates for inclusion in appropriately designated regional marine spatial planning.

We observed that foraging activity is restricted to the coastal areas. This localization may help to maximize net energy gain because coastal prey resources represent fairly predictable foraging habitat and also minimize travel costs (Austin et al. 2019, Afán et al. 2021). Females (Fig. 2) and males (Fig. 3) were both restricted to coastal movements and showed preferences for foraging in nearshore environments during reproduction and chick rearing in both 2017 and 2018. Using visual inspection of the kernel density estimation, we observed that foraging areas changed with the season but were similar within years. However, males undertook flights to more distant and equally productive areas to the south and north of Baja California Sur, crossing the peninsula and engaging in overland trips. For movements of males and females along the peninsula during the beginning of chick rearing in 2017, although some tracks show that individuals share the same areas, it is interesting to observe how males use sites to the north and south extensively, and they realize overland

Fig. 3. Maps of Baja California Sur showing Magnificent Frigatebird core foraging areas of males in 2017 (left panel) and 2018 (right panel). Blue polygons = 25% use distribution, purple polygons = 75% use distribution, dashed line = 100 m depth, dotted line = 250 m depth.



movements, especially southward, highlighting the sex-based movement behavior (Fig. 1). Traveling over land is not rare among seabirds. Arctic Terns (*Sterna paradisica*) migrate across the Andes and southern Argentina (Duffy et al. 2014). Boobies and albatrosses have been observed hundreds of kilometers inland (Anchundia et al. 2017), suggesting that some pelagic birds cross land voluntarily or due to environmental constraints. Over tropical waters, thermals produced by trade winds are generally used by soaring birds by day over land (Weimerskirch et al. 2003). Frigatebirds (*F. minor*, *F. magnificens*) and Blue-footed Boobies (*Sula nebouxii*) were observed crossing the Perry Isthmus of Isla Isabela, Galápagos (Anchundia et al. 2017), and we observed the continuous overland trips across the Baja California Sur peninsula undertaken by some Magnificent Frigatebird individuals nesting in Bahía San Gabriel and Santa Margarita Island, Mexico. On the southeast side of Veracruz, Magnificent Frigatebird individuals were seen soaring over hills and jungles in the middle of the Isthmus of Tehuantepec, flying overland from one ocean to the other (Dalquest 1951). Moreover, Magnificent Frigatebird adults were seen passing over the Central Desert in the north of Baja California, approximately 30 km from the Gulf of California and 58 km from the Pacific Ocean (Clark and Ward 1993). These observations suggest that this behavior is common, especially within the breeding season, when both pelagic and nearshore species of seabirds frequently range over extensive areas and cross multiple habitats (Jodice and Suryan 2010). Like most seabirds, Magnificent Frigatebirds are central-place foragers

during the breeding season, returning to land on a regular basis to incubate or feed nestlings (Jodice and Suryan 2010). The overland movements may represent trips between foraging and nesting sites.

We inferred that foraging habitat preferences indicate habitats with high nutrient concentrations because many seabirds forage in upwelling systems, where the movement of deep cold waters toward the surface creates a contrasting gradient in nutrient availability from highly productive colder areas to oligotrophic warmer waters (Zango et al. 2019). Although the most productive areas of the Gulf of California are located along its eastern side and in the northern region, due to winter upwelling and tidal mixing, respectively (Lluch-Cota 2000), the Bay of La Paz, in the southwestern part of the gulf, and the Magdalena Lagoon complex, located on the Pacific coast of Baja California Sur, represent exceptions. In the Bay of La Paz, the photosynthetic pigment concentrations remain high year-round compared to its surroundings, constituting an isolated spot of high phytoplankton biomass (Santamaría-del-Angel et al. 1994, Kahru et al. 2004). Seasonal oceanographic conditions in the bay, including surface mixing driven by northwesterly winds in winter (Badan-Dangon et al. 1991) and cyclonic circulation in summer (Monreal-Gómez et al. 2002, Sánchez-Velasco et al. 2006), cause increased nutrient supply to the base of the food web, attracting low trophic-level prey for planktivorous and piscivorous predators. The Magdalena Lagoon complex, with its geographic orientation and physical characteristics, creates a highly

productive and biologically diverse embayment (Bizzarro 2008). The shallow, protected waters of the Magdalen Lagoon complex are typically warmer, more quiescent, and more productive than the adjacent offshore waters (Acosta-Ruiz and Lara-Lara 1978, Lluch-Belda et al. 2000), creating prime nursery conditions for a variety of vertebrate and invertebrate taxa. This region is considered to have high primary productivity throughout the year, with similar phytoplankton abundance in the surface and subsurface waters (Gárate-Lizárraga et al. 2001). Phytoplankton blooms form a major energy base for animal populations higher in the food chain, including zooplankton, fish, marine mammals, and seabirds. Ecosystems with high phytoplankton concentrations are some of the most productive ecosystems in the world (Wynn and Knefelkamp 2004). Therefore, the high primary productivity year-round in the Magdalena Lagoon complex makes it an extremely important feeding area for frigatebirds.

The Gulf of California and Magdalena Lagoon complex are the most important fishing regions in Mexico (De-la-Cruz-Agüero et al. 1994, Obeso Nieblas et al. 1999, Lluch-Cota et al. 2007), and frigatebirds are often seen feeding on fishing waste, due to their surface and kleptoparasitic foraging style. Nearshore, frigatebirds can rely on more predictable coastal prey resources associated with static features and can target schooling fish that inhabit surface waters, such as flying fish and ballyhoo (Hazen et al. 2013). In addition, nearshore habitats require less travel time to access, and there are likely other factors involved in driving individuals to engage in coastal foraging. For example, predictable opportunities for kleptoparasitism occur in coastal waters that are adjacent to breeding colonies of other seabirds (i.e., Red-footed Boobies and Brown Boobies), even though the technique of parasitizing other seabirds near their grounds represents only a minor proportion of the food resource (Vickery and Brooke de 1994, Le Corre and Jouventin 1997).

In the case of Magnificent Frigatebirds, competition associated with size differences may be an underlying mechanism, with larger individuals (females) outcompeting smaller individuals (males) in nearshore waters (Trefry and Diamond 2017). This phenomenon might explain why males foraged on average further from the colony in our study. Different parental roles observed between the sexes might also be involved in shaping behavior. Female frigatebirds feed chicks more frequently and carry greater quantities of food than males during periods of biparental care (Calixto-Albarrán and Osorno 2000, Osorno and Székely 2004). Therefore, ties to the colony may be greater for females, who choose to minimize costs associated with commuting with a heavy food load during chick-provisioning trips (Cuthill and Kacelnik 1990). Males may therefore be freer to travel to profitable pelagic areas to forage. Alternatively, a trade-off may exist between size-mediated competition and levels of parental investment (Lagarde et al. 2004, Osorno and Székely 2004). Furthermore, interspecific competition is likely to be higher close to colonies, where the available pool of resources can become locally depleted by the population (Gaston et al. 2007). Another strategy used by many tropical seabirds to locate feeding opportunities is to associate with subsurface predators, especially tuna or dolphins (Au and Pitman 1986), that bring the prey close to the surface in the open ocean (Ballance and Pitman 1999) and coastal environments (Jaquemet et al. 2004) and also drive flying fish and squid out of the water and into the breaks of frigatebirds. Subsurface predators

support, at least in part, most species that feed in the tropics (Ballance and Pitman 1999), with a level of seabird community reliance on subsurface predators that is unparalleled compared to polar, temperate, and subtropical waters (Miller et al. 2018). Because of their close association, studies of the distribution of frigatebirds and subsurface predators such as tunas or dolphins (Weimerskirch et al. 2004) can be developed to preserve marine resources in poorly understood tropical oceanic waters.

Data on foraging ranges collected with bird-borne devices combined with ecological data such as indices of resource availability can produce accurate predictions of at-sea distributions of seabirds (Ronconi et al. 2012) and provide information about the areas where foraging behavior is most frequently observed. Recent developments in tracking technologies have made it possible to investigate patterns of seabird resource use at a level of detail never achieved before and over extended temporal periods. These developments present opportunities to reexamine questions that traditional methods have been unable to resolve (Mott et al. 2017). In particular, the delimitation of Mexican priority marine regions was based on two multidisciplinary workshops in 1998 (Arriaga-Cabrera et al. 2009). Criteria for establishing priority marine regions for conservation were defined by experts based on cartography obtained from coastal and oceanic biogeographic provinces, bathymetric charts, and federal and state natural protected areas (Arriaga-Cabrera et al. 2009), but no data about seabird distributions were integrated in the conservation planning due to lack of data.

CONCLUSION

Here, we provide three consecutive years of data on the foraging behavior of Magnificent Frigatebirds between the Gulf of California and the Mexican Pacific Ocean. The results come from information provided by GPS satellite telemetry, and no personal observations were included in the analysis. Our study includes cues on movement patterns and foraging habitat preferences during the reproductive and nonreproductive periods, showing that individuals tend to return to the same area on successive trips, displaying a high degree of predictability. Magnificent Frigatebirds seem to have a primarily coastal distribution (Diamond 1972), focusing on areas with higher productivity on a regional scale (Weimerskirch et al. 2004). Additionally, we observed that movement patterns and dispersion along the peninsula follow a seasonal rhythm with annual repeatability. There is evidence of sex-based differences in home range, with females using smaller core areas and rarely embarking on oceanic trips, instead foraging close to the colony or nearshore. For males, the presence of both coastal and pelagic feeding improve efficiency in resource exploitation and reduce intraspecific competition (Bolnick et al. 2003). Interaction between bathymetry and tidal currents appear to play a dominant role (Amélineau et al. 2016) in the consistency of the selection of foraging areas across seasons. Thus, bathymetry may provide a buffer against changes in other environmental variables such as sea surface temperature, suggesting that the ecological significance of biophysical structure stems from the capacity to alter prey density, distributions, and behavior, increasing accessibility for predators and enhancing their foraging efficiency (Amélineau et al. 2016). Changes occurring at the global level will

modify the environmental conditions of the habitat itself and may also alter prey abundance and availability (Hollowed et al. 2013). Under these circumstances, low predator plasticity could eventually compromise their ability to cope with environmental stochasticity and limit adaptive responses to global change (Reed et al. 2010). Plasticity in foraging behavior is not unexpected in tropical species such as frigatebirds because low productivity and patchy prey distributions characterize the environment in which they live. The ability to adapt to unpredictable conditions is highly advantageous in tropical waters, and many studies have reported flexible strategies in frigatebird species. However, our results show that individuals in the Baja California Sur colonies visit the same areas across years, with preferences for coastal prey resources. So, it is possible that foraging areas selected by frigatebirds are important sites of productivity and, consequently, food resources are available. Nevertheless, the decreasing numbers of individuals in this population could suggest less plasticity and limited ability to cope with global environmental changes. Our data on movement parameters and feeding areas are essential to evaluate the effectiveness of marine protected areas and contribute to regional marine spatial planning to expand or establish additional priority conservation areas outside those already existing and safeguard the resources needed by this species.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2202>

Acknowledgments:

We thank Parque Nacional Zona Marina del Archipiélago Espíritu Santo (PNZMAES) and Comisión Nacional de Áreas Naturales Protegidas (CONANP) for logistical assistance and availability. In particular, we thank Irma González López and Elia López Greene for their useful assistance, help, and support. All applicable national and institutional guidelines for the care and use of animals were followed. Fieldwork was carried out under permission numbers SGPA/DGVS/00321/16 and SGPA/DGVS/00404/17 from the Dirección General de Vida Silvestre (SEMARNAT). Particular thanks to all R-package developers and contributors for data analysis.

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