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Morgan Gilmour
University of California, Santa Cruz

José Castillo-Guerrero
Universidad de Guadalajara

Abram Fleishman
San Jose State University

Salvador Hernández-Vázquez
Universidad de Guadalajara

Hillary Young
University of California, Santa Barbara

See next page for additional authors

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Authors

Morgan Gilmour, José Castillo-Guerrero, Abram Fleishman, Salvador Hernández-Vázquez, Hillary Young, and Scott Shaffer

Plasticity of foraging behaviors in response to diverse environmental conditions

MORGAN E. GILMOUR¹,[†] JOSÉ A. CASTILLO-GUERRERO,² ABRAM B. FLEISHMAN,^{3,4}
SALVADOR HERNÁNDEZ-VÁZQUEZ,⁵ HILLARY S. YOUNG,⁶ AND SCOTT A. SHAFFER³

¹Ocean Sciences Department, University of California Santa Cruz, Santa Cruz, California 95060 USA

²CONACYT-Universidad de Guadalajara, Centro Universitario de la Costa Sur, San Patricio – Melaque, Cihuatlán, Jalisco 48980 México

³Department of Biological Sciences, San Jose State University, San Jose, California 95192 USA

⁴Conservation Metrics, Inc., 145 McAllister Way, Santa Cruz, California 95060 USA

⁵Departamento de Estudios para el Desarrollo Sustentable de Zona Costera, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Gómez Farías No. 82, San Patricio-Melaque, Cihuatlán, Jalisco 48980 México

⁶Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93106 USA

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Abstract. Due to rapidly changing global environmental conditions, many animals are now experiencing concurrent changes in both resource availability and the foraging cues associated with finding those resources. By employing flexible, plastic foraging strategies that use different types of environmental foraging cues, animals could adapt to these novel future environments. To evaluate the extent to which such flexibility and plasticity exist, we analyzed a large dataset of a clade (Sulidae; the boobies) of widespread aerial tropical predators that feed in highly variable marine habitats. These surface foragers are typical of many ocean predators that face dynamic and patchy foraging environments and use a combination of static and ephemeral oceanographic features to locate prey. We compared foraging habitats and behaviors of four species at seven colonies in the eastern and central Pacific Ocean that varied greatly in depth, topography, and primary productivity. Foraging behaviors, recorded by GPS-tracking tags, were compared to remotely sensed environmental features, to characterize habitat-behavior interactions. K-means clustering grouped environmental characteristics into five habitat clusters across the seven sites. We found that boobies relied on a combination of static and ephemeral cues, especially depth, chlorophyll-a concentrations, and sea surface height (ocean surface topography). Notably, foraging behaviors were strongly predicted by local oceanographic habitats across species and sites, suggesting a high degree of behavioral plasticity in use of different foraging cues. Flexibility allows these top predators to adapt to, and exploit, static and ephemeral oceanic features. Plasticity may well facilitate these species, and other similarly dynamic foragers, to cope with increasingly changing environmental conditions.

Key words: area restricted search; foraging habitat; foraging strategy; Gulf of California; k-means clustering; Northwestern Hawaiian Islands; oceanographic characteristics; Palmyra Atoll; *Sula dactylatra*; *Sula leucogaster*; *Sula nebouxii*; *Sula sula*.

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[†] **E-mail:** mgilmour@ucsc.edu

INTRODUCTION

Adaptive foraging behavior specific to an animal's morphology and its environment allow the

animal to navigate diverse landscapes while efficiently searching for food (Schoener 1971, Bal-lance et al. 1997). The degree to which animals can adapt to changes in the foraging cues of their

habitats is determined by their foraging strategies. Flexible and specialized foraging strategies are dependent on the stability of available resources (West-Eberhard 1989). Resources that are predictable on temporal and spatial scales enable specialization, and specialist strategies are advantageous because they reduce decision-making (Forister et al. 2012) and physiological costs (Webb 1984). Conversely, more variable ecosystems may produce unpredictable environmental conditions and patchy resources, and a generalist foraging strategy becomes advantageous because there are less constrained diet requirements and less specialized behaviors. Thus, adoption of a more flexible approach to foraging enables animals to efficiently navigate uncertain environments while gaining physiological, survivorship, and fitness benefits (Hadfield and Strathmann 1996). However, given today's rapidly changing environment, animals have been forced to adapt their behaviors rapidly to survive (Kearney et al. 2009, Wong and Candolin 2015).

In the context of current ecosystem changes around the globe, plasticity in foraging behaviors could be advantageous to many species experiencing changes in their environments (Beever et al. 2017). Indeed, flexible strategies enable animals to exploit novel habitats (Manenti et al. 2013). Variations in behaviors and habitat use are two mechanisms through which animals could employ flexible foraging (Jung and Kalko 2010). As habitats change, a flexible foraging strategy could vary the types of cues (static and ephemeral features) used within a habitat. Though traditional studies of behavioral plasticity have aimed to answer broad evolutionary questions that focus on the relationships between plasticity, fitness trade-offs, and genetic variance (Hadfield and Strathmann 1996, Chevin et al. 2010), changes in an animal's behaviors, habitat use, and diet are its immediate response to rapid environmental change (Van Buskirk 2012). These adaptations are especially important because ecosystem changes are occurring on multiple scales that range from immediate habitat alterations like deforestation (Jenkins et al. 2003) and dredging (Pirotta et al. 2013); episodic events like eutrophication (Phil et al. 1992) and pollution (Michalec et al. 2013); and long-term changes that include annual increases in temperature (Kearney et al. 2009),

introductions of invasive species (O'Dowd et al. 2003), and over-fishing (Jackson et al. 2001). It is essential to know how foraging behaviors change, and the degree to which animals rely on static vs. ephemeral foraging cues, at these different temporal scales. To assess animals' foraging plasticity in a changing environment, we characterized habitat-behavior interactions within the wide array of environmental conditions found in the variable marine ecosystem.

Marine habitats contain both static and ephemeral features that animals use to navigate and forage. For example, static cues like seamounts provide a permanent structure that upwells nutrients to surface water and provide a reliable location of nutrients and prey for upper trophic level predators (Ballance et al. 2006, Palacios et al. 2006). Ephemeral processes like currents that shift seasonally (e.g., the Costa Rica Dome; Fiedler 2002) and annually (Philander et al. 1996, Bograd et al. 2004) transport nutrients and plankton larvae. Thus, basic marine features like thermal structure, upwelling, currents, and bathymetric topography shape biological processes like primary productivity (Rutherford et al. 1999, Rykaczewski and Checkley 2008), and subsequently affect the distribution of many organisms like fishes and top predators throughout the year (Kwasniewski et al. 2010, Block et al. 2011, Elliott et al. 2014). The resulting habitat created by the combination of static and ephemeral oceanographic processes with patchy prey distributions may make foraging difficult for predators (Weimerskirch 2007). These challenges are further compounded for seabirds that typically hunt from the air to obtain subsurface prey like fishes and squids.

Seabirds that forage in the marine environment provide an excellent natural experiment with which to assess foraging plasticity in the face of constantly changing environmental conditions. Boobies (Sulidae) are tropical seabirds that inhabit coastal and pelagic habitats that differ greatly in topography, seasonality, and prey resources. Yet, they forage efficiently in these oceanic environments, employing similar feeding techniques throughout their cosmopolitan range. Boobies are central-place foragers when breeding and thus are constrained spatially and temporally while foraging (boobies forage 0.2–150 km from the nest during breeding; Weimerskirch et al. 2009, Kappes

et al. 2011, Young et al. 2015, Poli et al. 2017). Consequently, the constraints of central-place foraging allowed us to evaluate behavioral plasticity in an otherwise vast and ephemeral ocean. We analyzed global positioning system (GPS) tracking data from seven colonies in the eastern and central Pacific Ocean (Fig. 1) to examine the foraging ecology of four out of the six booby species from the genus *Sula*: Blue-footed (*Sula nebouxi*); Brown (*S. leucogaster*); Masked (*S. dactylatra*); and Red-footed (*S. sula*). Three of these species (Brown, Masked, and Red-footed) have a worldwide distribution, allowing the results of our study to extend to populations throughout the globe; though, regional oceanographic differences may also contribute to site-specific behaviors (Suryan et al. 2006). The large environmental variations between our study sites allowed us to fully assess potential differences that boobies encounter between colonies, and the degree to which they rely on static and ephemeral features to forage. Study sites included a semi-enclosed sea and coastal and pelagic regions, and varied greatly in depth, topography, and primary productivity (Appendix S1: Table S1). Boobies' behaviors such as distance traveled and foraging frequency would likely vary with the features of each of these habitats. For example, patches of chlorophyll on the ocean surface change in size with changes in plankton

community composition, nutrient availability, and predation (Haury et al. 1978). A chlorophyll patch that is present at a given time may move or disappear within 24 h, causing top predators like boobies to increase the size of their search area to compensate for the change in position, or absence, of the chlorophyll patch. Subsequently, the change in chlorophyll would change the distance traveled and the foraging frequency during their foraging trip. Given the rapidly changing environment for many species due to anthropogenic habitat alterations and climate change (Croxall et al. 2012, Wong and Candolin 2015), assessment of boobies' behavioral plasticity in response to a continuously changing ocean provides insight about inter- and intra-specific adaptability across a widely distributed clade.

Given the oceanographic differences surrounding our study colonies (Appendix S1: Table S1) and the potential for some oceanographic conditions like primary productivity to be ephemeral, we tested whether foraging behaviors differed between colonies based on differences in local oceanographic habitats. Using k-means clustering by partitioning, oceanographic characteristics (sea surface temperature [SST]; sea surface height [SSH]; chlorophyll-*a*; depth; slope; and bathymetric position index [BPI]) were characterized into distinct habitat groupings. We hypothesized that differences in oceanographic habitats would drive differences in behaviors between colonies, providing support for adaptive foraging behaviors. We predicted that as opportunistic, flexible foragers, boobies would (1) have high behavioral plasticity, illustrated by a correlation between behaviors and local habitats and (2) share similar foraging behaviors with conspecifics and congeners if they shared similar foraging habitat.

METHODS

Colonies and species

This study took place at seven booby breeding colonies throughout the central and eastern Pacific Ocean (Fig. 1) between 2007 and 2016 (Table 1). Tracking data were collected from four booby species: Blue-footed, Brown, Masked, and Red-footed during the incubation and chick-brooding stages (Table 1). Males and females were distinguished by either vocalizations (Blue-footed and Masked; Nelson 1978), plumage (Brown; Nelson 1978),

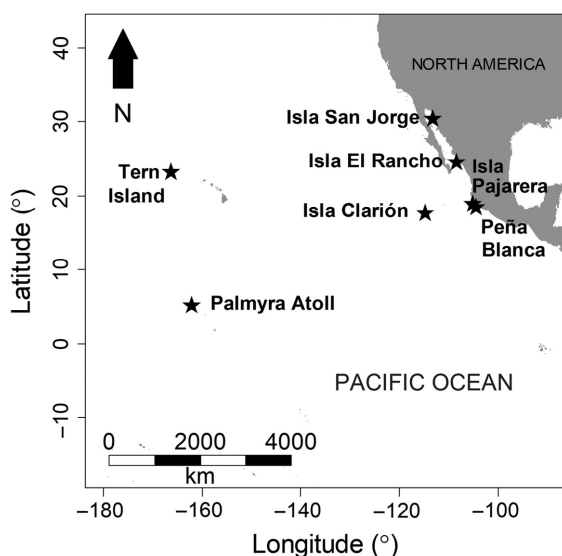


Fig. 1. Map of study sites (black stars) of foraging habitats and behaviors of booby species, 2007–2016.

Table 1. Summary of tracking data of booby foraging trips.

Colony and species	Tracking period (MM/YYYY)	Sex			Breeding stage			No. foraging trips (No. GPS pts)
		F	M	unk	I	B	unk	
Peña Blanca								
BRBO	10/2015	1	2	0	0	3	0	11 (2785)
	11/2015	1	1	0	1	1	0	6 (2811)
	05–06/2016	6	7	0	0	13	0	107 (21,085)
Isla Pajarera								
BRBO	06–07/2016	6	5	0	1	10	0	87 (13,994)
Isla El Rancho								
BFBO	02–05/2015	5	13	0	9	9	0	31 (5677)
	03/2016	6	5	0	0	11	0	15 (2643)
Isla San Jorge								
BRBO	02/2015	4	8	0	6	6	0	15 (5155)
Isla Clarión								
MABO	01/2016	1	2	0	3	0	0	5 (1218)
RFBO	01/2016	0	0	4	3	1	0	6 (3993)
Tern Island								
MABO	03/2009	8	3	0	11	0	0	14 (4769)
	02–03/2010	7	9	0	16	0	0	16 (8700)
	03/2012	8	7	0	15	0	0	16 (6057)
RFBO	03/2009	0	3	0	3	0	0	3 (2569)
	03/2010	3	2	0	5	0	0	5 (3781)
	03/2012	4	4	0	8	0	0	8 (5381)
Palmyra Atoll								
BRBO	08–09/2010	3	4	0	4	3	0	20 (4636)
	07–09/2014	1	3	2	2	4	0	19 (3675)
MABO	11/2008	7	5	1	3	9	1	29 (4856)
	09/2010	4	2	0	3	3	0	16 (4286)
RFBO	06/2007	0	1	0	0	0	1	1 (13)
	09/2007	0	1	0	1	0	0	1 (798)
	10/2008	6	1	1	7	0	1	8 (4164)
	09/2010	2	2	2	4	0	2	7 (2969)

Notes: Species abbreviations are BFBO, Blue-footed Booby; BRBO, Brown Booby; MABO, Masked Booby; RFBO, Red-footed Booby. Breeding stage indicates whether tracked bird was incubating eggs (I), brooding chicks (B), or if breeding stage was unknown (unk).

body mass (Masked and Red-footed), where females are larger than males within the pair (Nelson 1978, Weimerskirch et al. 2006), or through molecular analyses (Young et al. 2010); though, sex could not be determined for 10 birds (Table 1).

Instrumentation

Foraging movements were recorded with GPS-tracking tags (either iGot-u GT-120; Mobile Action Technology, New Taipei City, Taiwan; or GPS CatTrack1, Catnip Technologies, Anderson, South Carolina, USA). Tags were encapsulated in polyolefin for waterproofing. The total tracking package mass was 22 g, which was 1.1–1.9% of the body mass of the four booby species (mean mass Blue-footed: 1532 ± 258 g, $n = 60$; Brown:

1200 ± 189 g, $n = 70$; Masked: 1998 ± 276 g, $n = 41$; Red-footed: 1155 ± 167 g, $n = 36$). Birds were captured either by hand or net. Tags were taped underneath the central two to three tail feathers with waterproof tape (Tesa #4651, Hamburg, Germany). The duration of tag deployment varied between colonies and species; typically, a tag was either programmed to (1) start recording at 06:00, due to the diurnal behaviors of many booby species or (2) programmed to begin recording upon tag attachment to the bird. The sampling interval of the tags also varied between study sites, and ranged 1–120 s. Due to logistical differences between study sites, tags were deployed for 1–9 d, resulting in some individuals having multiple recorded trips.

GPS data processing

GPS-tracking tags recorded locations with high precision (10–60 s) and accuracy (~3 m), and thus, these data required minimal pre-processing. All track analyses and statistics were conducted in the program R (R Core Team, 2016, version 3.3.2) with custom-built functions, unless otherwise specified. Tracks were manually inspected to remove erroneous locations. Two simple speed filters were then employed to remove additional erroneous locations. First, a speed filter of 150 km/h was applied to remove erroneous locations, but allow for fast bursts of speed (Zavalaga et al. 2010). Second, because each species has different mean travel speeds, an additional forward-backward speed filter was applied, based on the mean maximum speed per species from these tracking data (mean maximum speeds: Blue-footed: 85 km/h; Brown: 82 km/h; Masked: 93 km/h; Red-footed: 91 km/h), using the function `vmask` from the R package `argosfilter` (Freitas 2012). Overall, <1% of raw GPS points were removed from any foraging track. Finally, all points within a 1-km polygon buffer around study colonies were excluded from analyses, following Kappes et al. (2011) and Young et al. (2015), because boobies do not forage within 1 km of nests (Weimerskirch et al. 2009, Poli et al. 2017).

To compare behaviors among tracked birds with different sample intervals, tracks were interpolated to one position every 60 s using the R package `adehabitatLT` (Calenge 2006). All distances were calculated with great circle distance (distance measured on a sphere) using the `distHaversine` function from the R package `geosphere` (Hijmans 2017a).

Behavior metrics

Trip-length metrics were calculated for each foraging trip. Five parameters described overall foraging behavior: mean travel speed; trip duration; total distance traveled; maximum distance from the colony; and foraging trip pattern (trip type). Three metrics of foraging activity were also identified: total foraging bouts; proportion of time spent on the water; and landings per hour. Landings were identified as locations where the flight speed was <5 km/h (Young et al. 2010). Landing locations often occurred consecutively, so to calculate the number of distinct foraging bouts, consecutive landing points were

grouped into one foraging bout. Foraging bouts separated by more than 60 s were considered separate foraging bouts, and the total number of foraging bouts was calculated for each foraging trip. The proportion of time spent on water was calculated as the total time spent foraging divided by the total duration of the foraging trip. Two foraging trip patterns were identified (“focused” and “throughout”; Appendix S1: Fig. S1) by manually inspecting each foraging track for landing points in relation to the furthest point from the colony. Foraging trips that had landing points only at the furthest points from the colony were labeled “focused” trips (e.g., Visscher and Seeley 1982; Appendix S1: Fig. S1a); additionally, focused trips included trips where <5 landing points were identified elsewhere along the trip. Foraging trips that had >5 landing points outside the furthest region were labeled “throughout” trips (Appendix S1: Fig. S1b).

Fidelity index

To assess the degree to which boobies used similar foraging areas among successive foraging trips, a Fidelity Index was estimated using an equation modified from Willis-Norton et al. (2015), Hazen et al. (2016), and Shaffer et al. (2017). The Fidelity Index compares the GPS location that is the furthest distance from the colony between successive foraging trips of one individual. The index is a value between –1 and 1; a value of 1 indicates high similarity of furthest locations between trips, and a value of –1 indicates no similarity. The Fidelity Index was obtained by the equations:

$$\text{delta distance} = \left| \frac{\text{distance}_i - \text{distance}_j}{\text{distance}_i} \right| \quad (1.1)$$

$$\text{delta angle} = \left| \text{angle}_i - \text{angle}_j \right| \quad (1.2)$$

$$\text{delta distance}_{cs} = 1 + \frac{\text{delta distance}}{-1} \quad (1.3)$$

$$\text{delta angle}_{cs} = \frac{(\text{delta angle} - 90)}{-90} \quad (1.4)$$

$$\text{Fidelity Index} = \frac{(\text{delta distance}_{cs} + \text{delta angle}_{cs})}{2} \quad (1.5)$$

where distance_{*i*} and distance_{*j*} are the great circle distances between the distal point of a foraging trip and the breeding colony; angle_{*i*} and angle_{*j*} are the bearings to the distal points of foraging trips (Eqs. 1.1 and 1.2). Distance and angle calculations were centered to have a mean of 0 and scaled so that they ranged between -1 and 1 (Eqs. 1.3 and 1.4). To enable scaling, Eq. 1.3 was multiplied by 1 or -1 if the value was positive or negative, respectively. The Fidelity Index was then calculated as the sum of the distance and angular displacements, and scaled so that it ranged -1 to 1 (Eq. 1.5). The Fidelity Index returns a bimodal scale that indicates the degree of similarity or difference between two trips' distal points. Values >0 indicate that two distal points are within 90° of each other, with a maximum value of 1 indicating that these two points are also the same distance from the colony. Values <0 indicate that two distal points are $>90^\circ$ apart, with a value of -1 indicating that the distal points are in opposite directions (180° displacement) and are a large distance apart. The Fidelity Index was calculated for all trip combinations, and the values were averaged to obtain one Fidelity Index value per bird.

Habitat variables

Oceanographic variables like SST, chlorophyll-*a* concentrations, SSH, depth, slope, and BPI were used to describe foraging habitat. In order to interpret boobies' habitat use, habitat variables were categorized as either static (depth, slope, BPI) or ephemeral (SST, chlorophyll-*a*, SSH). These variables are commonly associated with at-sea feeding aggregations for many marine predators (Ballance et al. 2006, Spear et al. 2007). Gradients of SST aggregate prey and therefore SST can be used to predict seabird foraging habitat (Mugo et al. 2014). Chlorophyll-*a* forms the base of the food chain via primary productivity and can attract feeding aggregations; thus, it is also an important predictor of seabird foraging habitat (Palacios et al. 2006, Kappes et al. 2010). Sea surface temperature and chlorophyll-*a* data were downloaded for each GPS location from the Aqua Spacecraft Moderate Resolution Imaging Spectroradiometer (MODIS; NASA's Goddard Space Flight Center, OceanColor Web 2017), via the *xtracto* function from the R package *xtractomatic* (Mendelssohn 2018). These datasets are 8-d composites of satellite-derived data, with resolutions of 2.7 km,

downloaded from an equal angle grid of 0.025° latitude by 0.025° longitude. Chlorophyll-*a* data were log-transformed after download (hereafter referred to as chlorophyll). Sea surface height is a measure of ocean surface topography, and SSH is a proxy for upwelling regions and eddies, which bring nutrient-rich water to the surface and enhance primary productivity. Sea surface height data were obtained as hourly means from 0.0833° latitude by 0.0833° longitude grids from a 14-d hindcast model from AVISO satellites via the Copernicus Marine Environment Monitoring Service (E. U. Copernicus Marine Service Information 2017). Depth and slope are commonly used to identify upwelling regions that exhibit high primary productivity in the marine environment. The BPI is a type of terrain index that quantifies the absolute difference between a cell's depth and the mean depth of the surrounding eight cells, and determines whether the location forms part of a bathymetric crest or trough (Wilson et al. 2007). Positive and negative BPI values indicate that the point is higher or lower than its average surrounding points, respectively. Bathymetry data for the variable depth were obtained from the NOAA dataset "ETOPO1" via the R package *marmap* (Pante and Simon-Bouhet 2013). Slope and BPI were calculated from the depth data, using the R package *raster* (Hijmans 2017b).

Principal components analysis

Principal components analyses (PCA) and k-means clusters by partitioning were used to characterize the marine habitat for each foraging trip. This method simplified the six habitat variables into linear combinations via PCA and grouped the environmental patterns via k-means clustering to classify and visualize habitat groupings; this approach has been used on a variety of data types including fisheries and oceanographic data (Plaza et al. 2017), materials engineering (He and Tan 2018), and marine mammal behavioral data (Robinson et al. 2007). Principal components analyses is a standard and commonly used tool in oceanographic science (Preisendorfer and Mobley 1988). Principal components analyses was conducted on three sets of data: (1) the GPS locations from the entire foraging trip (full-trip); (2) transit locations; and (3) landing locations to characterize foraging habitat separately. The PCAs were conducted on the variables SST,

chlorophyll, SSH, depth, slope, and BPI with the `prcomp` function from the R package `stats` (R Core Team 2016). Each of the six variables were centered and scaled prior to PCA. Principal components whose eigenvalues were ≥ 1.0 were retained. These principal components were saved and used in k-means clustering analysis.

K-means clusters by partitioning

The optimal number of centroids for k-means was chosen following Schreer and Testa (1995) and Robinson et al. (2007). First, successive k-means clustering analyses were run on the three retained principal components using two to 20 clusters. Second, the *F*-statistic from each cluster analysis was plotted against the number of clusters. The resulting scree plots helped to determine that five clusters represented the most variation among the clusters for all three sets of data, and groupings larger than five did not further describe the variance in each analysis. Therefore, the k-means clustering analysis was conducted using five centroids and 25 random starts with the function `k-means` in the R package `stats` (R Core Team 2016).

The k-means analysis assigned a cluster to each GPS location. Though nearly half of the foraging trips had GPS locations that were assigned to a single full-trip cluster, more than half of the foraging trips had GPS locations in multiple full-trip clusters. To use foraging trips that had multiple full-trip clusters in behavioral analyses, full-trip clusters were combined into a singular categorical variable. For each foraging trip, full-trip clusters were ranked by the proportions of time that a bird spent in each cluster. For example, a bird that traveled within full-trip clusters 1, 3, and 5, and spent 45%, 20%, and 35% of the trip in each cluster, respectively, would be assigned the full-trip cluster category 1.5300. Thus, the cluster number before the decimal refers to the cluster in which an individual spent the most time, and the cluster numbers after the decimal refer to clusters in which less time was spent, but still visited. This assignment method ultimately resulted in 15 unique full-trip cluster combinations across 444 foraging trips.

Statistical models of behavior

Linear mixed effects models (LMEs) with restricted maximum likelihood were used to test

whether foraging behaviors and full-trip clusters were related. The significance of the fixed factors of the LME was assessed with ANOVA with Type III sum of squares. Because the trip type variable was binomial, a logistic regression with a logit link was used to test whether trip type was correlated with clusters. Each behavior metric (travel speed; total distance traveled; trip duration; maximum distance from colony; total foraging bouts; proportion of time spent on the water; landing rate) was the response variable in separate LMEs; full-trip cluster, species, sex, and the interaction term species:full-trip cluster were fixed factors; and, to avoid any effects of pseudoreplication, individual bird number was used as a random factor, nested in year (Sommerfeld et al. 2013, Mendez et al. 2015). Sex was included as a fixed factor because behavioral differences have been observed in boobies due to reverse size sexual dimorphism (females are larger than males; Weimerskirch et al. 2006, 2009, Castillo-Guerrero and Mellink 2011, however, Zavalaga et al. 2007, Young et al. 2010, and Kappes et al. 2011 did not observe sex-based differences in flight behaviors). Similarly, species was a fixed factor because the four booby species differ in size (see mean body masses per species in Instrumentation section). Only cluster combinations with >10 trips were included in these analyses. Linear mixed effects models were conducted with the function `lmer` from the R package `lme4` (Bates et al. 2015); ANOVAs were conducted with the function `ANOVA` from the R package `car` (Fox and Weisberg 2011); and logistic regression was conducted with the function `glm` from the R package `stats` (R Core Team 2016).

Response variables for LMEs were visually inspected with histograms and Q-Q plots to test for normality: Travel speed was normally distributed; maximum distance from colony and total landings were log-transformed; total distance traveled, trip duration, proportion of time spent on water, and landing rate were square root-transformed. Therefore, the error structures for these variables approached normal distributions, and a Gaussian family was selected for all models. Significance of models were assessed at $P < 0.05$.

We tested the predictions that there would be (1) different behaviors in different habitats, represented by significant relationships between behaviors and full-trip clusters and (2) similar

foraging behaviors between conspecifics and congeners within habitats, represented by non-significant interaction terms of species:full-trip cluster.

RESULTS

Environmental characteristics

A total of 444 foraging trips by 183 individual birds were analyzed (Table 1). Oceanographic habitat characteristics for foraging trips were described by a combination of PCA and k-means cluster analyses. For the full-trip dataset, the first three principal components explained 40.7%, 20.0%, and 17.3% of the variance, respectively. The first three principal components of the transit points explained 41.0%, 19.3%, and 17.7% of the variance, respectively. Similarly, the first three principal components from the landings dataset explained 40.4%, 21.4%, and 16.7% of the variance, respectively. Both static and ephemeral features had large loading values in the PCA, especially chlorophyll, depth, and SSH (Table 2).

Foraging habitat was significantly different from transit habitat (Appendix S1: Table S2). However, landing and transit locations were grouped similarly by their oceanographic characteristics (Fig. 2). To illustrate the oceanographic habitats of foraging trips, the full-trip and landing clusters were overlaid on maps of foraging trips (Figs. 3, 4). Cluster 1 was the deepest (median depth \pm SE: 3566 ± 10 m; $n = 34,507$ points) and

coldest (median SST \pm SE: $22.9 \pm 0.01^\circ\text{C}$; $n = 34,507$ points; Fig. 2), and it occurred only at the pelagic colonies (Isla Clari3n, Palmyra, and Tern Island; Figs. 3, 4). Cluster 2 was characterized by the highest slope (median slope \pm SE: $7.9 \pm 0.04^\circ\text{C}$; $n = 9939$ points) and highest BPI (median BPI \pm SE: 50.3 ± 0.45 ; $n = 9939$ points), indicating that it had complex bottom topography (Fig. 2). Cluster 3 was unique to the coastal Mexican colonies of Isla Pajarera and Pe3a Blanca (Figs. 3, 4) and had the warmest SST (median SST \pm SE: $30.0 \pm 0.01^\circ\text{C}$; $n = 31,715$ points) and high chlorophyll (median chlorophyll-*a* \pm SE: 0.44 ± 0.002 mg/m³; $n = 31,715$ points; Fig. 3). Cluster 4 had deep (median depth \pm SE: -3166 ± 7.4 m; $n = 20,670$ points), warm (median SST \pm SE: $28.4 \pm 0.01^\circ\text{C}$; $n = 20,670$ points) water with high slope (median slope \pm SE: $6.32 \pm 0.03^\circ$; $n = 20,670$ points; Fig. 2). Cluster 5 was unique to the Gulf of California (Figs. 3, 4) and was the shallowest (median depth \pm SE: -16 ± 0.26 m; $n = 12,461$ points) with the highest chlorophyll (median chlorophyll-*a* \pm SE: 2.49 ± 0.01 mg/m³; $n = 12,461$ points) and no slope (median slope \pm SE: $0.09 \pm 0.01^\circ\text{C}$; $n = 12,461$ points; Fig. 2).

Behaviors

Travel speed, total distanced traveled, trip duration, maximum distance traveled from the colony, total foraging bouts, and landing rate were correlated with full-trip clusters and species (Table 3). The proportion of time boobies spent on the water (Table 3) and trip type (logistic regression: $P = 0.316$, $\chi^2 = 9.32$, $\text{df} = 8$, $n = 423$) were not correlated with the full-trip clusters. The fixed factor species was not correlated with landing rate or the proportion of time spent on the water, and the fixed factor sex was only correlated with total distance traveled (Table 3). The interaction term species:full-trip cluster was not a significant factor for any behaviors except for trip duration (Table 3). Behaviors ranged widely between clusters (Table 4) and between species and colonies (Appendix S1: Table S3).

The Fidelity Index indicated that boobies from all colonies exhibited a medium to high degree of site fidelity among foraging trips (Fidelity Index: 1.54 ± 0.74 ; range: 0.15–4.24; $n = 78$ birds; Fig. 5), suggesting that boobies tended to re-visit foraging locations during successive foraging trips.

Table 2. Loadings of components for each environmental variable on the first three principal components from the full dataset (all GPS points; $n = 109,292$).

Environmental variable	Component loadings		
	PC 1	PC 2	PC 3
Depth	0.46	−0.16	0.29
Chlorophyll	0.60	0.09	−0.10
SSH	− 0.57	0.15	0.12
SST	0.10	− 0.78	0.06
Slope	−0.31	− 0.56	0.14
BPI	0.04	0.17	0.93

Notes: Variables that have the greatest magnitude of regression coefficients in each principal component are highlighted in bold. Abbreviations are SSH, sea surface height; SST, sea surface temperature; and BPI, bathymetric position index. PC1 is most strongly correlated with chlorophyll, SSH, and depth. PC2 is most strongly correlated with SST and slope. PC3 is most strongly correlated with BPI.

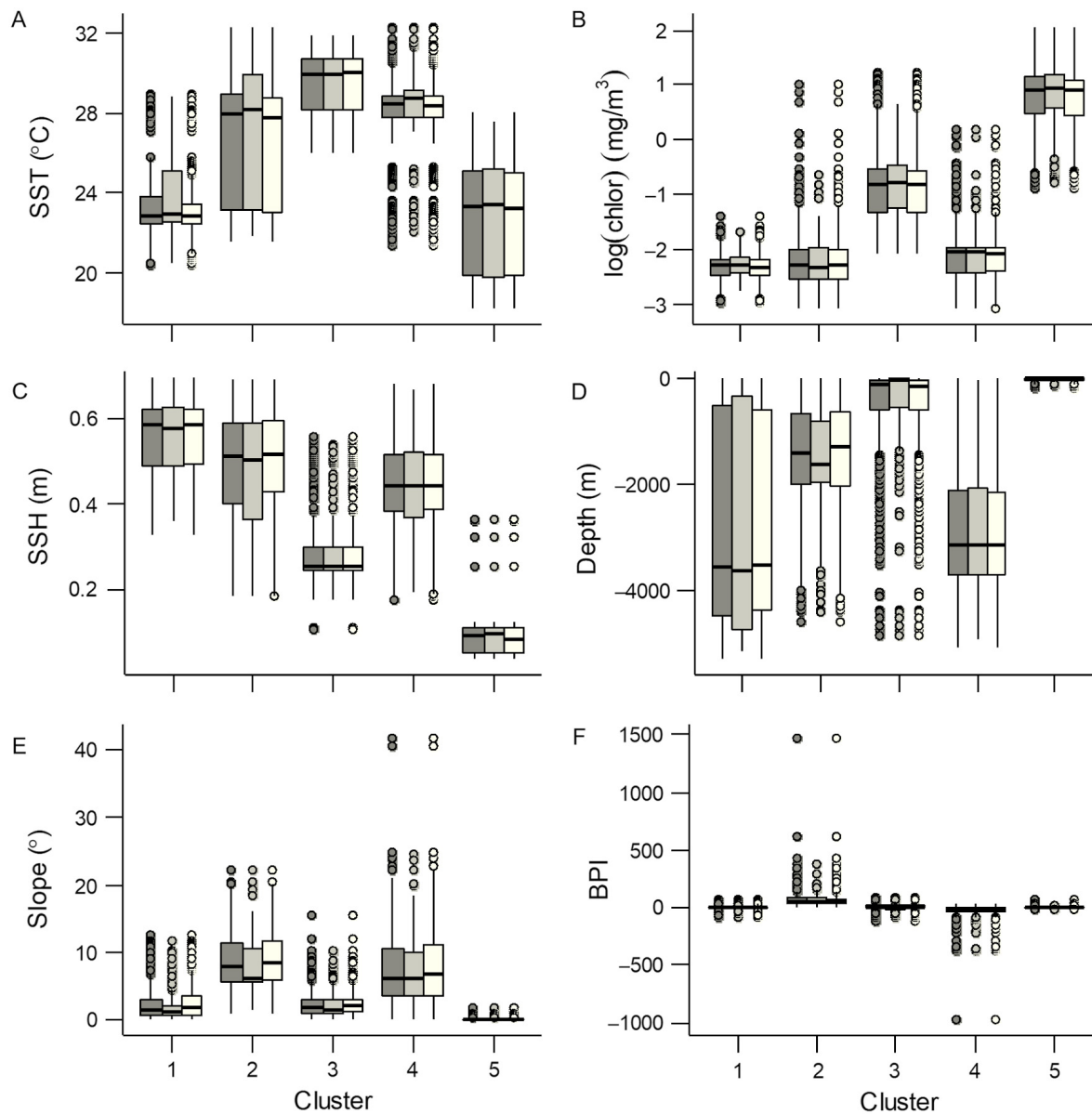


Fig. 2. Boxplots representing summary statistics of oceanographic habitat clusters from overall foraging trips (dark gray boxes), and from foraging habitat (light gray boxes) and transit habitat (white boxes). Clusters were identified by k-means clusters by partitioning of the first three principal components retained from PCA on (A) sea surface temperature (SST), (B) chlorophyll, (C) sea surface height (SSH), (D) depth, (E) slope, and (F) bathymetric position index (BPI; the difference between the peak/trough of one point and the surrounding eight points) of all locations ($n = 109,292$ points), landing locations ($n = 34,032$ points), and transit locations ($n = 75,260$ points) from booby foraging trips. Horizontal bars represent the median, and vertical bars represent \pm SE.

DISCUSSION

Foraging behaviors of seven populations of a clade of aerial marine predators were strongly

predicted by local oceanographic habitats, supporting our hypothesis that boobies exhibit adaptive foraging behaviors in a wide range of habitats. The significant relationships between

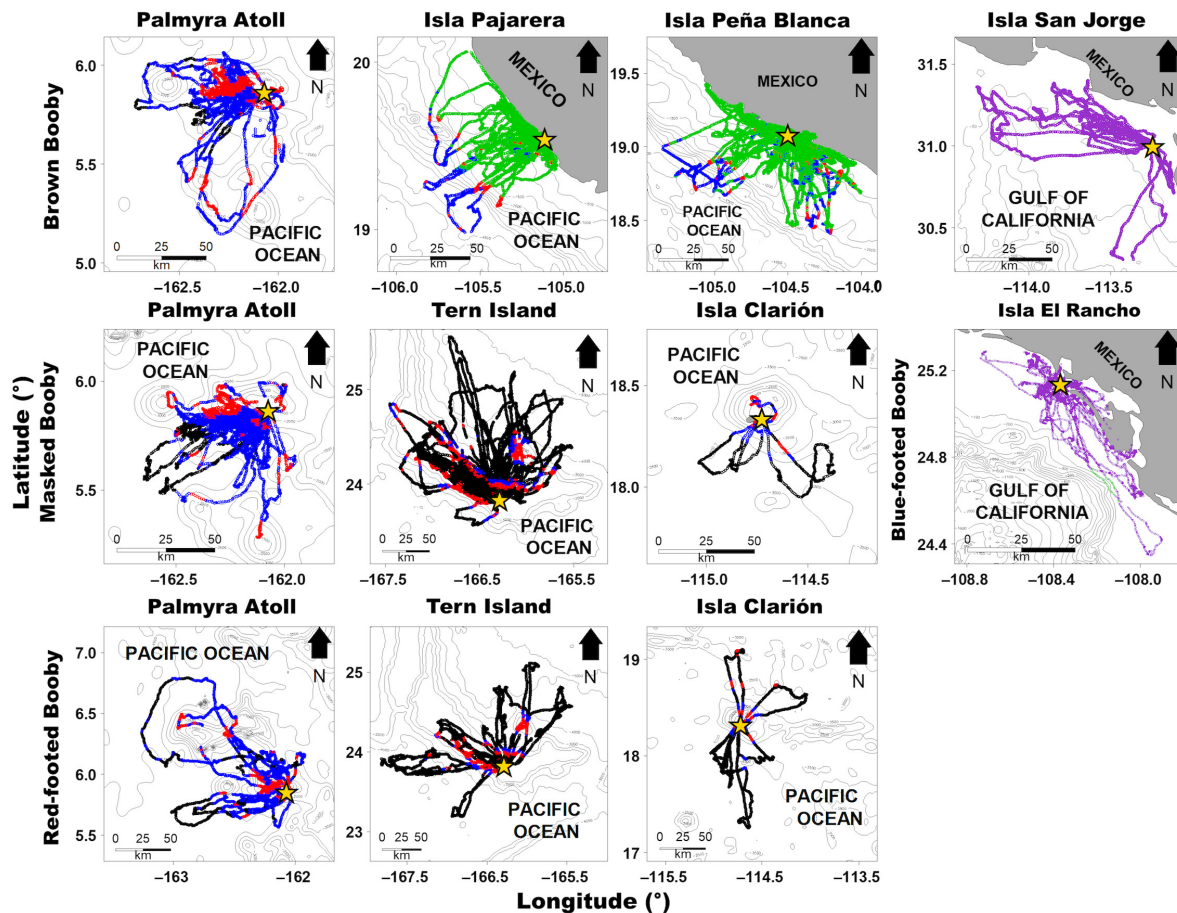


Fig. 3. Maps of boobies' foraging trips, colored by full-trip cluster (colored circles). Study species are listed by row, and study colonies are listed by column. Colonies are represented by yellow stars. Solid gray corresponds to land. Gray lines correspond to bathymetry (m); contour intervals vary between colonies: The contour interval for Isla San Jorge is 50 m; for Isla El Rancho is 100 m; for Isla Clarión, Isla Pajarera, Palmyra Atoll, and Peña Blanca is 500 m; and for Tern Island is 1000 m. Full-trip cluster colors: black circles, cluster 1 (cold, deep pelagic cluster); red circles, cluster 2 (shallow pelagic cluster with complex bottom topography); green circles, cluster 3 (high chlorophyll coastal cluster); blue circles, cluster 4 (warm, deep pelagic cluster); purple circles, cluster 5 (benthic Gulf cluster).

most behaviors and full-trip cluster supported our first prediction that behaviors were different in different habitats. The interaction term of species:full-trip cluster was not a significant factor for any behaviors except trip duration, supporting our prediction that individuals shared behaviors with conspecifics and congeners if they shared similar habitat. Oceanographic habitats were composed of a combination of static and ephemeral features, especially depth, chlorophyll, and SSH, illustrating that boobies exhibit foraging plasticity in response to complex and

unpredictable environments. Adaptability to changing environmental conditions is important in the context of rapidly changing environmental conditions, including a potential future of novel environments due to anthropogenic habitat alterations and climate change (Croxall et al. 2012, Beever et al. 2017).

Environmental drivers of foraging behaviors

Foraging plasticity arises in response to differing environmental conditions (West-Eberhard 1989). In this study, environmental conditions

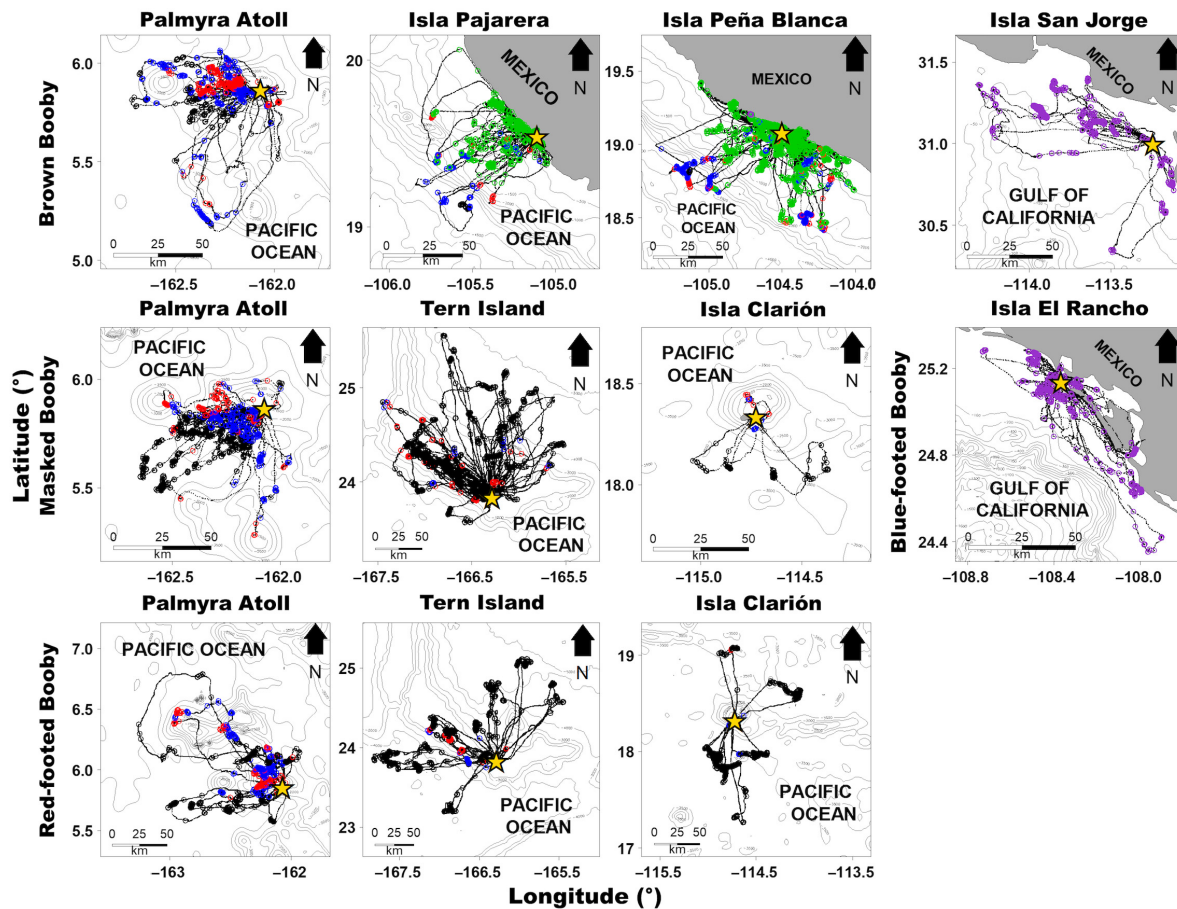


Fig. 4. Maps of boobies' foraging trips (black dots) and foraging events (open circles) colored by landing cluster. Study species are listed by row, and study colonies are listed by column. Colonies are represented by yellow stars. Solid gray corresponds to land. Gray lines correspond to bathymetry (m); contour intervals vary between colonies: The contour interval for Isla San Jorge is 50 m; for Isla El Rancho is 100 m; for Isla Clarión, Isla Pajarera, Palmyra Atoll, and Peña Blanca is 500 m; and for Tern Island is 1000 m. Landing cluster colors: black circles, cluster 1 (cold, deep pelagic cluster); red circles, cluster 2 (shallow pelagic cluster); green circles, cluster 3 (high chlorophyll coastal cluster); blue circles, cluster 4 (warm, deep pelagic cluster); purple circles, cluster 5 (benthic Gulf cluster).

varied across seven study colonies, creating the potential for localized differences in behaviors. Four colonies had environmental characteristics unique to their respective regions: Isla Pajarera and Peña Blanca formed a cluster of warm, shallow water and high chlorophyll in southern coastal Mexico (cluster, 3); and Isla San Jorge and Isla El Rancho formed another cluster that was shallow, flat, and had low SSH (cluster 5) in the Gulf of California. Variations in static and ephemeral features can lead to differences in prey distributions and availability (Pierce et al. 2008), and together, habitat and diet cause

differences in foraging behaviors in predators (Wong and Candolin 2015). For example, shallow, flat habitat at Islas San Jorge and El Rancho could provide highly profitable foraging areas for three reasons. First, the northern Gulf of California experiences large diurnal tidal changes (up to 9 m). During low tide, boobies in the northern Gulf of California have access to benthic prey in addition to schooling prey, leading to boobies' diverse diet (Mellink et al. 2001). Second, reliable prey sources in shallow regions could result from seasonal wind-driven upwelling along the coast that drives high productivity

Table 3. Assessment of significance of fixed effects (obtained via type 3 ANOVA tests) from linear mixed effect models, where booby behaviors were response variables, and habitat cluster, species, sex, and the interaction of species:full-trip cluster were predictor variables.

Behavior	<i>n</i>	Cluster			Species			Sex			Species:Cluster		
		χ^2	df	<i>P</i>	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Travel speed	430	16.2	8	0.040	8.8	3	0.032	4.8	2	0.092	1.9	8	0.983
Total distance traveled	430	65.1	8	<0.001	20.1	3	<0.001	7.8	2	0.020	14.4	8	0.073
Trip duration	430	42.9	8	<0.001	30.9	3	<0.001	2.6	2	0.273	19.4	8	0.013
Max. distance	430	49.3	8	<0.001	13.1	3	0.004	5.2	2	0.073	5.8	8	0.671
Total foraging bouts	422	17.1	8	0.029	28.7	3	<0.001	1.0	2	0.610	14.6	8	0.067
Landing rate	422	16.4	8	0.037	2.6	3	0.463	5.4	2	0.068	2.9	8	0.940
Proportion time on water	422	12.5	8	0.131	2.1	3	0.556	4.7	2	0.096	5.5	8	0.708

Notes: Bird number was nested in sample year as random factors. All response variables (except travel speed) were transformed prior to analyses to meet assumptions of normality: Maximum distance and total foraging bouts were log-transformed, and total distance traveled, trip duration, landing rate, and proportion of time spent on water were square root-transformed.

Table 4. Summarized booby behaviors (mean \pm SD) from foraging trips per cluster category, where each category represents the proportion of time a bird spent in each of five full-trip cluster habitats.

Cluster category	No. trips	Travel speed (km/h)	Total distance traveled (km)	Trip duration (h)	Maximum distance (km)	No. foraging bouts	Landing rate (landings/h)	Proportion time on water (%)
1	59	25 \pm 8	212 \pm 121	8.7 \pm 5.5	82 \pm 44	47.0 \pm 39.2	6.2 \pm 5.0	26.7 \pm 15.1
1.2	11	24 \pm 7	170 \pm 110	7.1 \pm 4.5	70 \pm 47	34.7 \pm 31.8	4.7 \pm 2.4	27.5 \pm 15.4
1.4	6	20 \pm 5	155 \pm 62	7.9 \pm 3.0	59 \pm 26	48.0 \pm 20.2	6.2 \pm 1.8	38.8 \pm 15.0
2	3	9 \pm 7	8 \pm 12	0.5 \pm 0.7	7 \pm 5	6.3 \pm 7.5	22.7 \pm 15.3	48.5 \pm 27.3
2.1	1	19	235	12.5	77	103.0	8.3	30.5
2.4	13	20 \pm 6	85 \pm 51	5.5 \pm 5.9	29 \pm 17	29.5 \pm 25.5	5.9 \pm 1.8	31.9 \pm 20.3
3	192	20 \pm 8	56 \pm 43	2.8 \pm 1.9	22 \pm 16	20.8 \pm 14.5	8.3 \pm 4.4	34.6 \pm 21.3
3.4	13	27 \pm 6	164 \pm 66	6.0 \pm 2.1	64 \pm 21	35.5 \pm 25.7	5.45 \pm 3.13	18.4 \pm 11.1
3.5	1	16	56	3.5	27	32.0	9.1	47.9
4	47	24 \pm 8	67 \pm 45	2.9 \pm 2.2	30 \pm 16	20.3 \pm 21.0	6.4 \pm 3.5	27.8 \pm 21.8
4.1	11	25 \pm 6	147 \pm 101	6.4 \pm 4.1	59 \pm 33	33.3 \pm 28.7	5.2 \pm 2.3	24.0 \pm 14.8
4.2	23	25 \pm 7	104 \pm 71	4.7 \pm 3.4	40 \pm 25	27.0 \pm 21.7	5.6 \pm 2.6	23.0 \pm 18.4
4.3	2	22 \pm 3	232 \pm 25	10.9 \pm 2.6	85 \pm 5	87.0 \pm 36.8	7.8 \pm 1.5	35.3 \pm 0.2
4.32	1	29	142	4.9	57	16.0	3.3	9.2
5	61	23 \pm 9	75 \pm 69	3.6 \pm 3.4	31 \pm 26	19.6 \pm 27.5	5.0 \pm 2.7	31.1 \pm 19.8

(Lavín and Marinone 2003). Third, estuarine and terrestrial input near Isla El Rancho likely provide high productivity and many foraging opportunities (Hidalgo-González and Alvarez-Borrego 2004). Additionally, estuaries in the Gulf of California are nurseries for many fish species, providing another seasonal food source for predators (Zetina-Rejón et al. 2003). Together, the drastically different habitat and diversity of available prey in the Gulf of California likely contributes to behavioral differences compared to boobies in other regions.

Ecological niches shifted in the three pelagic colonies, where environmental characteristics

formed three habitat clusters that were shared among colonies that were more than 1000 km apart (clusters 1, 2, and 4). Isla Clarión, Palmyra Atoll, and Tern Island are located in tropical and subtropical pelagic waters, where productivity is typically low, and foraging opportunities for seabirds may be limited (Weimerskirch 2007). However, these pelagic habitats predicted foraging behaviors. The deepest cluster (cluster 1) was not present at the coastal colonies, distinguishing the deep, pelagic water from other types of booby foraging habitat in this study. Deep cluster 1 occurred at the furthest points of foraging trips, where boobies likely rely heavily on subsurface

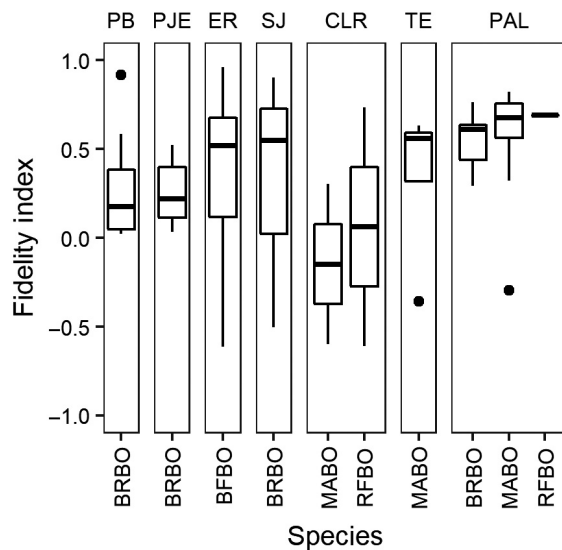


Fig. 5. Boxplots of fidelity index of boobies that had at least two foraging trips ($n = 78$ birds). Fidelity index ranges from no fidelity (-1) to high fidelity (1). Species abbreviations are BFBO, Blue-footed Booby; BRBO, Brown Booby; MABO, Masked Booby; RFBO, Red-footed Booby. Colony abbreviations are CLR, Isla Clarión; ER, Isla El Rancho; PAL, Palmyra Atoll; PB, Peña Blanca; PJE, Isla Pajarera; SJ, Isla San Jorge; TE, Tern Island. Bars represent median \pm SE.

predators like dolphins and tuna to drive prey to the surface in these deep waters (Scott and Catanch 1998, Bertrand et al. 2002, Spear et al. 2007). Clusters 2 and 4 were shallower than cluster 1 and had higher slopes, which suggest upwelling conditions. For example, Brooks Banks is a shoal to the northwest of Tern Island, and Masked and Red-footed Boobies frequently foraged along its edges (cluster 4; Young et al. 2015). This type of upwelling habitat was also important across several colonies: Brown Boobies at Palmyra Atoll mostly used clusters 2 and 4—the clusters that are also shared with Brown Booby foraging habitat at the Isla Pajarera and Peña Blanca colonies. Upwelled water created by shoals aggregates nutrients and prey species, and provides an important, reliable foraging habitat for Brown Boobies. Thus, across all colonies, boobies adapted to their regional foraging habitats to forage most efficiently. This is especially evident for five of the seven colonies that each had three clusters: Boobies could forage in three habitat types that contained a mix of static

and ephemeral features, but to forage most efficiently, they chose to either search for subsurface predators in deep water (cluster 1), or focused on upwelling regions that aggregated prey (clusters 2 and 4).

Evidence for behavioral plasticity

Animals modify foraging behaviors to optimize energy expenditure with the amount of energy obtained from food (Schoener 1971, Stephens and Krebs 1986, Sims et al. 2008). To maintain this energy balance, animals use cues to find food. Across the seven study sites, boobies exhibited variations in behaviors, and these behaviors were strongly correlated with local oceanographic habitats. To forage efficiently within these varied habitats, boobies used a combination of static (depth) and ephemeral (chlorophyll, SSH) environmental cues to find food. Boobies also likely used visual cues (e.g., seeing other predators foraging in groups, Au and Pitman 1986, tracking oceanographic features like eddies and fronts, Tew Kai and Marsac 2010) and internal cues (e.g., returning to places that previously had food, Irons 1998; and indicated by high site fidelity indices) while foraging. By using these environmental, visual, and internal cues across study sites, boobies demonstrated behavioral plasticity in relation to local environmental conditions.

Local oceanographic conditions determined whether boobies transited or foraged in a region: Foraging and transit habitats were significantly different, and foraging bouts and landing rates were predicted by full-trip clusters. Additionally, landing rates were not predicted by either species or sex. Together, this strongly suggests that foraging activity is determined by local oceanographic conditions, specifically the presence of upwelled water. Foraging bouts and landing rates were highest in upwelling conditions (clusters 3 and 2, respectively) and lowest in regions that were more influenced by diurnal tidal changes than upwelling (cluster 5 for both behaviors). Upwelling may continually provide prey aggregations, allowing for easy foraging, and thus cause boobies to land frequently. These foraging behaviors are likely driven by localized oceanographic conditions that also drive prey species' distributions (e.g., Pierce et al. 2008). Many foraging bouts and/or high landing rates could represent a large prey patch, where a bird

lands frequently in an area full of food, like in the middle of schooling fish at the surface (Sommerfeld et al. 2015). Alternatively, high landing frequencies could imply scarce prey, because individuals repeatedly landed to capture prey and foraging effort was therefore high. The ability to adjust foraging activity to local conditions and high or low prey densities greatly aids predators' adaptability to acute and chronic environmental changes (e.g., Jung and Kalko 2010).

Behaviors related to overall foraging effort (total distance traveled, duration, speed) reflected the amount of time and energy an individual exerted to find food. These behaviors were predicted by full-trip cluster, demonstrating that local oceanographic characteristics are an important factor during optimal foraging. For example, boobies may follow the edges of eddies like other tropical seabirds (Tew Kai and Marsac 2010) in shallow habitats with high chlorophyll, like cluster 3, which is unique to Isla Pajarera and Peña Blanca. Alternatively, a lack of external cues could cause a bird to transit through the habitat quickly: Cluster 4 had low chlorophyll and birds that spent the most time in cluster 4 had fast travel speeds and few foraging bouts. This behavior indicates that boobies are more likely to transit through this habitat type to get to a more preferred habitat type, such as cluster 2 (shallow pelagic cluster with complex bottom topography), which had an overall large landing rate (indicative of foraging activity). Similarly, short trip durations took place in association with cluster 3 (high chlorophyll coastal cluster). Short foraging trips close to these colonies may indicate reliable food sources that birds frequently exploit.

The maximum distance metric represented the furthest point at which a foraging booby parent traveled searching for food while maintaining an energy balance (energy expenditure during self-foraging and chick-provisioning, for example) and optimal flight-energy efficiency (Schoener 1971). Therefore, the habitat clusters identified at the furthest points of long trips suggest that these locations were preferable environments that provided predictable foraging opportunities. The largest mean maximum distance traveled was in cluster 1 (cold, deep pelagic cluster), indicating that traveling to this habitat type was worth the energy expenditure to get there. This is further supported by boobies' medium-high site fidelity,

where individuals were likely re-visiting profitable foraging habitat. However, our fidelity index varied between colonies, and is also in opposition to other studies that have observed low site fidelity in boobies in the Indian Ocean (Masked and Red-footed boobies; Weimerskirch et al. 2005, Kappes et al. 2011). Site fidelity in boobies may be related to the predictability of local static and ephemeral cues used at each colony. A high proportion of static (and thus predictable) foraging cues could aid in high site fidelity at one colony, whereas a high proportion of ephemeral cues could indicate low site fidelity at another colony. Indeed, the Indian Ocean is warmer and less productive than our study areas in the Pacific Ocean, and foraging conditions are less predictable (Weimerskirch 2007, Kappes et al. 2011).

Restrictions on behavioral plasticity

Differences in body size, physiology, and age may have constrained plasticity of some behaviors. Though plasticity allows animals to function within a range of environmental conditions, physiological factors such as morphology or energy reserves limit animals' capacity for behavioral plasticity (Cooke et al. 2013). Body size varied among the four booby species and between sexes. Thus, body size likely affected flight aerodynamics and diving dynamics (Ropert-Coudert et al. 2004, Kappes et al. 2011) and foraging locations (Young et al. 2010), and may have affected boobies' capacities for behavioral plasticity. For example, a larger body size would enable females to sustain flight for longer distances than males, and in fact, the only behavior predicted by sex was the total distance traveled. The physiological capacity and behavioral plasticity of females to sustain longer flight than males may be advantageous during periods of low food abundance and may ultimately result in better fitness (Hadfield and Strathmann 1996). The opposite trend was observed between species however: Brown and Red-footed Boobies had the smallest body masses, but Blue-footed and Brown Boobies generally had shorter trips than Masked and Red-footed Boobies. This is additionally supported by the significance of the interaction term of species:full-trip cluster for trip duration. The amount of time spent at-sea may be dependent on local oceanographic differences

between colonies (Suryan et al. 2006). Overall, some behaviors may be restricted by physiological and morphological capacities, but in this study, inter-specific differences in body size were less important than habitat: This result is consistent with observations that Masked and Red-footed Boobies forage in pelagic regions >50 km from the colony (Young et al. 2010, Mendez et al. 2017).

Age and experience may also affect behavioral plasticity. Long-lived species accumulate a lifetime of responses to chronic environmental changes and may be more adaptable to future changes (Beever et al. 2017). In this study, trip type was not predicted by habitat. Trip type in boobies may be influenced by internal factors like experience and age, where older, more experienced individuals are more likely to make focused trips instead of searching for prey along the entire length of the trip (Rutz et al. 2006). Older, more experienced individuals may also recognize foraging cues more readily and thus know when to alter their behaviors to forage efficiently (Zimmer et al. 2011).

CONCLUSIONS

Behaviors were strongly predicted by local oceanographic habitats. These habitats were shared across colonies and species, demonstrating that boobies exhibit great behavioral plasticity. Environmental features that were most prominent in our analyses were both ephemeral (chlorophyll; SSH; SST) and static (depth; slope), reflecting short- and long-term variations in the marine environment. Together, this suggests that as environmental conditions change, boobies could adjust to new conditions. Flexibility of foraging behaviors to seasonal and variable oceanographic conditions is helpful for birds facing changing climates and habitat destruction (Croxall et al. 2012), and changes to nesting habitat availability (Mannocci et al. 2014). For example, low-lying nesting colonies are at risk of disappearing due to rising sea levels (Croxall et al. 2012, Hatfield et al. 2012). If forced to re-locate to new nesting areas, boobies would adapt and be able to forage efficiently in potentially new environments. However, some animals may have less flexible foraging ecologies due to physiological (Webb 1984), reproductive (Boersma and

Rebstock 2009), and life history (Abrams 1991) constraints. New environmental regimes could have high foraging effort costs that alter body condition and population dynamics (Wong and Candolin 2015). We suggest that foraging behavioral plasticity in relation to these constraints should be investigated on large scales of populations, species, and clades to assess the degree to which species could adapt to future environmental perturbations.

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