



# Carotenoid skin ornaments as flexible indicators of male foraging behavior in a marine predator: Variation among Mexican colonies of brown booby (*Sula leucogaster*)

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## Abstract

Carotenoid-dependent ornaments can reflect animals' diet and foraging behaviors. However, this association should be spatially flexible and variable among populations to account for geographic variation in optimal foraging behaviors. We tested this hypothesis using populations of a marine predator (the brown booby, *Sula leucogaster*) that forage across a gradient in ocean depth in and near the Gulf of California. Specifically, we quantified green chroma for two skin traits (foot and gular color) and their relationship to foraging location and diet of males, as measured via global positioning system tracking and stable carbon isotope analysis of blood plasma. Our three focal colonies varied in which foraging attributes were linked to carotenoid-rich ornaments. For gular skin, our data showed a shift from a benthic prey-green skin association in the shallow waters in the north to a pelagic prey-green skin association in the deepest waters to the south. Mean foraging trip duration and distance of foraging site from coast also predicted skin coloration in some colonies. Finally, brown booby colonies varied in which trait (foot versus gular skin color) was associated with foraging metrics. Overall, our results indicate that male ornaments reflect quality of diet and foraging—information that may help females select mates who are adapted to local foraging conditions and therefore, are likely to provide better parental care. More broadly, our results stress that diet-dependent ornaments are closely linked to animals' environments and that we cannot assume ornaments or ornament signal content are ubiquitous within species, even when ornaments appear similar among populations.

**Keywords** Skin color · Environmental variation · Dynamic sexual traits · Foraging · Carotenoids · Seabirds

## Introduction

While sexual ornaments are widespread among animals, understanding how they evolve and are used in mate choice remains a major challenge (Olson and Owens 1998; Cornwallis and Uller 2010; Hill et al. 2023). Recently, considerable attention has focused on the mechanisms of honesty in carotenoid ornaments: pigment-based features common among birds, reptiles, and fish, that are often associated with measures of individual quality (Olson and Owens 1998; McGraw 2006; Pérez-Rodríguez 2009; Weaver et al. 2017; Hill et al. 2019, 2023). Most animals cannot synthesize carotenoid pigments de novo and must therefore obtain them through diet (McGraw 2006). The rarity hypothesis proposes that when animals' dietary carotenoids are limited—as is likely for carnivores—they can use carotenoid ornaments to signal diet quality and foraging ability, as only skilled

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foragers should be able to obtain sufficient carotenoids for high-quality ornaments (Olson and Owens 1998). Indeed, manipulative studies show that altered carotenoid consumption can limit or enhance ornament expression in several species (Velando et al. 2006; Leclaire et al. 2019; Biswas et al. 2023). In addition, a growing body of literature demonstrates diet can predict naturally occurring variation in carotenoid ornament quality, primarily in carnivorous species where dietary carotenoids are deposited directly into skin with little or no physiological alteration (Negro et al. 2002; Casagrande et al. 2009; Michael et al. 2018; Leclaire et al. 2019). Diet-linked carotenoid ornaments may be particularly useful sources of information for current and potential mates in species with biparental care. Skilled foragers will likely provision offspring more effectively, and an ornament that can signal diet and foraging ability would be highly informative for mate choice and reproductive investment decisions.

Many sexual ornament studies assume that ornament traits and their signal content are conserved across populations. However, carotenoid ornaments are likely prone to environmentally driven, intraspecific variation because of their association with diet and foraging behaviors and their origin in autotrophs. The diets and optimal foraging behaviors of animals are, themselves, heavily influenced by environment and prone to spatial variation, including marked differences between populations of the same species (Garduño-Paz and Adams 2010; Wiley et al. 2019; Romano et al. 2021). In addition, carotenoids are synthesized primarily by autotrophs for use as accessory photosynthetic pigments, with carotenoid types and concentrations largely driven by environmental light exposure (e.g., location in the water column) (Bianchi et al. 1997; Bonilla et al. 2005). Therefore, we should expect that certain spatial gradients, such as those in water depth or dominant primary producer taxa, will result in pronounced and persistent shifts in the availability of carotenoids to the rest of the food web. For example, a study of guppies (*Poecilia reticulata*) showed that a gradient of light availability altered the dietary availability of carotenoid pigments and the expression of sexual coloration in males (Grether et al. 1999). More broadly, we expect that carotenoid availability to animals is closely linked to the food webs and ecosystems in which they forage, as well as the particular diet items they ingest. We hypothesize that for carotenoid ornaments to convey useful information about diet and foraging behavior to mates and potential mates, they must have a flexible relationship to diet that is able to shift geographically in concert with carotenoid availability and optimal diet and foraging behaviors. In other words, the signal content of carotenoid ornaments—the particular diet and foraging behaviors associated with carotenoid-rich coloration—should be variable among populations.

Here, we test our hypothesis and study the dietary underpinnings of carotenoid ornaments in the brown booby (*Sula*

*leucogaster*), a marine predator that forages within and near the Gulf of California across a gradient in depth (an environmental parameter closely tied to carotenoid availability). Male brown boobies display blue to green-colored gular (throat) and green-yellow foot skin to their current and potential mates. These traits result from the deposition of largely unaltered, yellow dietary carotenoids on top of a structural blue coloration (Montoya et al. 2018). Importantly, green skin ornaments in males appear indicative of high quality in two *Sula* species: previous research on the brown booby and closely related blue-footed booby (*Sula nebouxii*) shows that green-turquoise coloration is preferred by females and associated with higher chick growth, chick survival, paternal provisioning rates, and female reproductive investment (Velando et al. 2006; Montoya and Torres 2015).

On Islas Marietas, Mexico, the skin color of courting male brown boobies is closely tied to their foraging behavior, with greener (more carotenoid-rich) gular skin linked to and apparently driven by foraging farther off-shore on a pelagic diet (Michael et al. 2018). However, brown boobies have a wide, pantropical distribution, and populations show localized preferences for different fish species (Mellink et al. 2001; Castillo-Guerrero et al. 2016). In the present study, we investigate male brown booby diet and foraging behaviors and their association with gular and foot skin color across three breeding colonies near the Gulf of California. Our focal colonies are distributed along a natural environmental gradient. Isla de San Jorge, in the far north of the Gulf of California, is surrounded by relatively shallow foraging areas (< 200 m). Isla San Pedro Mártir lies in the middle of the Gulf of California, near the shelf break and in areas of dramatic depth changes (50–2,000 m). Farthest to the south, Islas Marietas are positioned outside the Gulf of California. We use global positioning system (GPS) tracking and stable carbon isotope analyses of blood plasma to detail booby foraging behavior and the relative contribution of pelagic versus benthic carbon to diet over roughly 10 days—the time-scale at which brown booby skin color can change (Hobson and Clark 1993; Montoya et al. 2018). Because optimal foraging behaviors, diet, and carotenoid availability are likely to vary across our focal populations, we predict that the particular diet and foraging behaviors associated with carotenoid-rich skin ornaments will shift significantly across our populations, echoing the environmental gradient over which boobies forage.

## Methods

We studied three colonies of brown booby from Islas Marietas (hereafter referred to as Marietas,  $n = 16$ ; July to August 2016), Isla San Pedro Mártir (hereafter referred to as San

Pedro,  $n=44$ ; January to February 2018), and Isla de San Jorge (hereafter referred to as San Jorge,  $n=17$ ; December 2016—January 2017) Mexico, during the incubation and chick-rearing phases of breeding. Notably, individual ornament quality in brown boobies is repeatable throughout the breeding season (Montoya et al. 2018) and foraging-ornament relationships persist through courtship, non-breeding, and multiple years on Islas Marietas (Michael et al. 2018).

To measure foraging behavior and habitat use at sea, we tracked brown boobies from each colony for 6–10 days using miniature GPS tags (refer to Supplementary Materials for tag attachment and data analysis specifics). Foraging locations were identified by annotating foraging trip paths with behavioral state classification (resting, transiting, and searching) based on the Residence in Space and Time algorithm (Supplementary Materials). We used tracking data to (1) quantify foraging trip duration and total distance traveled (hereafter flight distance) on unique foraging trips (as indicators of foraging behavior), and (2) measure ocean depth and distance to coast at foraging locations (two physical variables describing the environment). The mean values of tracking metrics per individual were used for the analyses.

To evaluate skin color, we measured the reflectance of two brown booby skin traits: gular and feet. Measurements were taken upon recapture of birds using a handheld spectrophotometer (MINOLTA CM 2600d, Osaka, Japan), which collected reflectance spectra at 10-nm intervals from 360 to 740 nm (details in Supplementary Materials). A target mask of 8 mm in diameter was used for all measurements, and before every measurement session the device was calibrated against a standard white calibration plate and a zero target (the measuring port is directed to the air pointing to the grown). For each bird and each skin trait, three sequential measurements of nonoverlapping patches of the skin were taken while maintaining the spectrophotometer perpendicular to the skin surface and making sure that no external light entered. The average of these three measurements was automatically calculated by the device and was used to obtain the spectra data to calculate a green chroma variable (sum of reflectance from 480 to 550 nm/sum of reflectance from 360 to 700 nm) for the gular and the foot regions (Fig. 1S; Montoya and Torres 2015). Color data from five males of San Jorge were lost due to spectrophotometer error during field work, hence final sample size for color analyses was 12 for San Jorge. Notably, birds were captured for color measurement and GPS tag deployment during the night or early morning/late afternoon to diminish disturbance to the birds and the colony, and to diminish thermal stress for the birds.

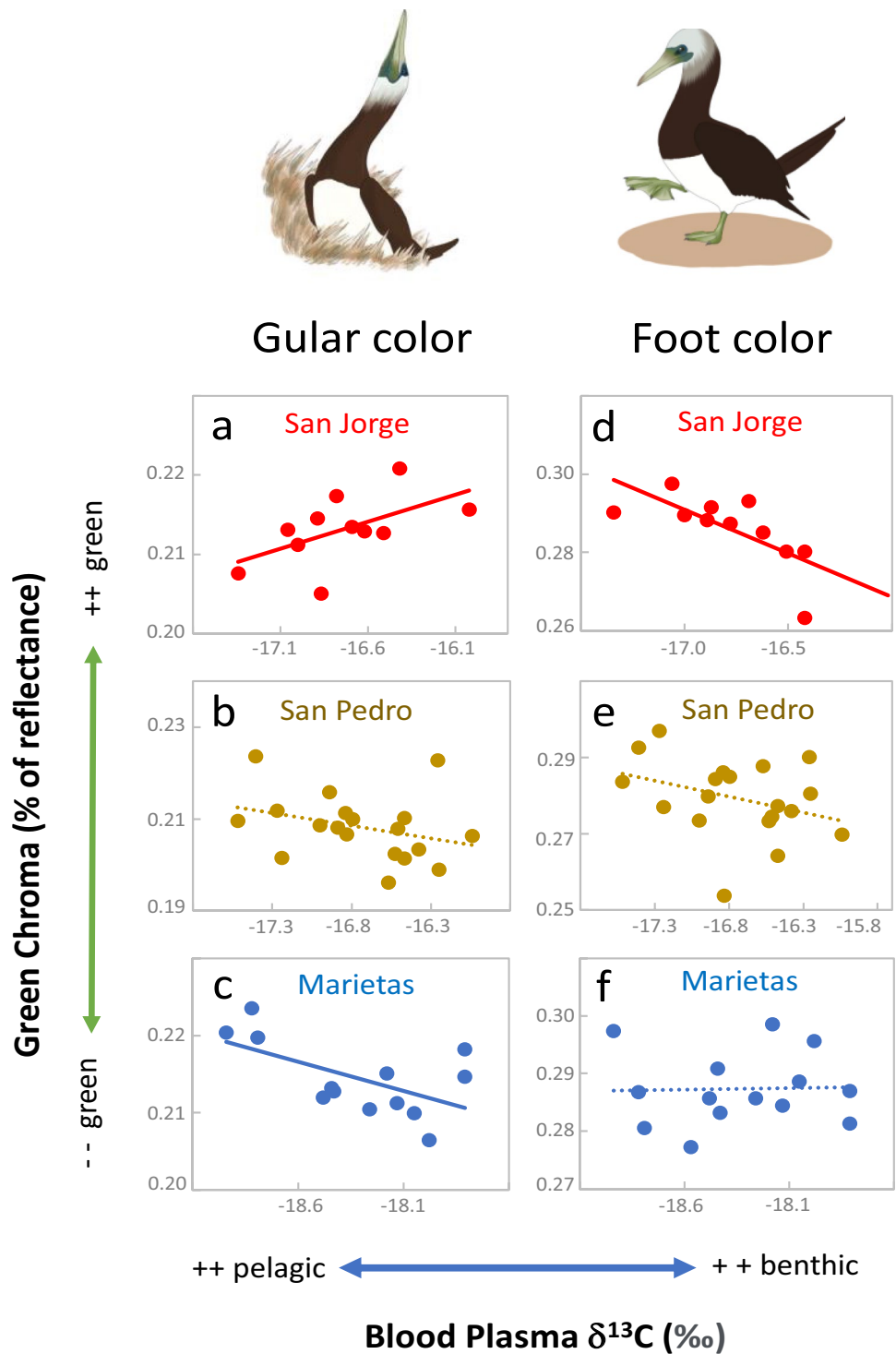
For a subsample of tracked brown boobies, we analyzed the stable carbon isotopic composition of blood plasma, which was collected from birds upon retrieval of GPS tracking devices (San Jorge  $n=17$ , San Pedro Mártir  $n=20$ , Marietas  $n=14$ ). Stable carbon isotope values in brown booby blood

plasma likely reflect diet over approximately 10 days (Hobson and Clark 1993) and therefore match the period of tracking. Blood sample collection and storage are described in the Supplementary Materials. Plasma samples were analyzed for their stable isotope composition on an elemental analyzer (Vario PYRO Cube, Elementar Americas) interfaced with an isotope ratio mass spectrometer (Isoprime 100). All isotope data are reported as per mil (‰) as dictated by  $\delta$  notation, given the equation:  $\delta^{13}\text{C} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$ , where  $R$  denotes the ratio of  $^{13}\text{C}/^{12}\text{C}$ , and the standard is Vienna Pee-dee belemnite. Laboratory standards were analyzed for  $\delta^{13}\text{C}$  between every 10 unknowns, with a precision of less than or equal to 0.1 ‰.

## Statistical analyses

We used independent linear models first to assess differences between colonies on foraging parameters, diet (estimated by plasma  $\delta^{13}\text{C}$ ) and gular and foot color and second, to evaluate the relationship between skin color (gular and foot color) and stable isotope data and tracking metrics. All variables were standardized within colony (standardized value =  $X - \mu / \sigma$ ) before the analyses to satisfy the linearity and homoscedasticity criteria, which were tested using the Shapiro–Wilk normality test and the studentized Breusch–Pagan test, respectively. To facilitate interpretation, we converted  $\delta^{13}\text{C}$  values to positive numbers (by adding 18.9, the absolute value of the lowest  $\delta^{13}\text{C}$  value) before standardization. Because data from San Pedro Mártir included males during the incubation and chick rearing period, gular and foot color were standardized according to breeding stage. Tracking data and  $\delta^{13}\text{C}$  from males sampled during incubation and chick rearing from San Pedro Mártir did not differ (Table S1 in Supplementary Materials), so no breeding stage-specific standardization was needed for these variables. To test the prediction that environmental heterogeneity influences the link between skin color and diet or foraging habits, models included either the standardized gular or foot color as response variables and as explanatory variables, the standardized tracking variable or  $\delta^{13}\text{C}$ , the colony, and the interaction between the two explanatory variables. Tukey's honestly significant difference tests (Tukey's HSD) were used to test whether slopes were significantly different from zero. Outliers were tested using the Bonferroni Outlier Test. Linear models were performed using the package nlme in R (Pinheiro et al. 2023). All statistical analyses were conducted in R version 4.2.1 (R Core Team 2022).

**Fig. 1** The relationship between male brown booby gular or foot color and blood plasma  $\delta^{13}\text{C}$  in three brown booby colonies nesting at Isla de San Jorge (a, d), Isla San Pedro Mártir (b, e), and Islas Marietas (c, f). Standardized values of all variables were used in independent linear models. Solid adjusted regression lines indicate slopes significantly different from zero. Drawings depict male brown boobies displaying carotenoid-dependent gular color during sky-pointing and foot skin color during parading. Artwork by Nathan Michael



**Results**

**Environmental heterogeneity and foraging behavior**

In accordance with the expectation that environmental variation among focal colonies would influence optimal foraging

behaviors and diet, all brown booby foraging parameters and diet (estimated by plasma  $\delta^{13}\text{C}$ ) differed between colonies (Table 1). On average, males from Marietas and San Pedro used mean foraging locations 2.4 times farther from the coast, made foraging trips that were 1.6 times longer, flew 2.3 times farther, and foraged over waters that were 32.2 times deeper compared to males from San Jorge (Table 1).

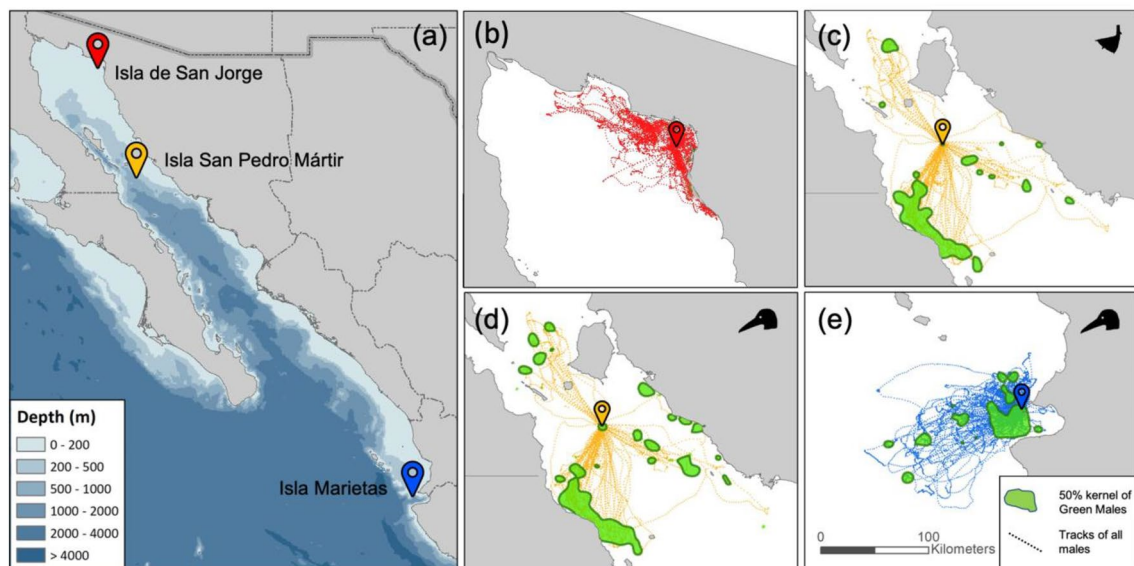
**Table 1** Variation in diet (measured via blood plasma  $\delta^{13}\text{C}$ ) and foraging behavior of male brown boobies across three breeding colonies: Isla de San Jorge, Isla San Pedro Mártir and Islas Marietas, México

Variable	Mean $\pm$ SD	<i>F</i>	<i>p</i>	$R^2_{adj}$
Distance to the coast of foraging location (km)				
Isla de San Jorge	11.92 $\pm$ 4.10	32.73	0.0001	0.45
Isla San Pedro Mártir	23.45 $\pm$ 6.32			
Islas Marietas	34.14 $\pm$ 13.28			
Trip duration (h)				
Isla de San Jorge	1.45 $\pm$ 0.43	13.45	0.0001	0.36
Isla San Pedro Mártir	2.33 $\pm$ 0.43			
Islas Marietas	2.18 $\pm$ 0.55			
Flight distance (km)				
Isla de San Jorge	90.43 $\pm$ 30.72	38.08	0.0001	0.49
Isla San Pedro Mártir	231.17 $\pm$ 55.92			
Islas Marietas	185.49 $\pm$ 81.00			
Depth at foraging location (m)				
Isla de San Jorge	- 26.32 $\pm$ 9.27	65.88	0.0001	0.62
Isla San Pedro Mártir	- 450.34 $\pm$ 174.65			
Islas Marietas	- 1243.39 $\pm$ 623.75			
$\delta^{13}\text{C}$				
Isla de San Jorge	- 16.96 $\pm$ 0.52	51.01	0.0001	0.66
Isla San Pedro Mártir	- 16.81 $\pm$ 0.50			
Islas Marietas	- 18.33 $\pm$ 0.35			

In addition, Marietas males had lower plasma  $\delta^{13}\text{C}$  values compared to males from the other two colonies, indicating a heavier reliance on pelagic food chains and prey, which have lower  $\delta^{13}\text{C}$  compared to their benthic counterparts (Table 1). Male gular and foot color during the chick rearing period did not differ between colonies (gular green chroma  $F_{2,35} = 0.56$ ,  $P = 0.58$ ; foot green chroma  $F_{2,34} = 1.47$ ,  $P = 0.24$ ; Fig. 2S).

### Skin color and plasma $\delta^{13}\text{C}$

Supporting our focal prediction, the relationship between brown booby gular color and blood plasma  $\delta^{13}\text{C}$  varied in direction and magnitude between colonies (Table 2). On Marietas, males with greener gular color had relatively low  $\delta^{13}\text{C}$  values, indicating more pelagic diets, and a weaker version of the same trend was found in San Pedro (Table 2, Fig. 1b,c). In contrast, males with greener gulars from San Jorge had higher  $\delta^{13}\text{C}$  values and presumably, diets richer on benthic prey compared to duller-colored males (Fig. 1a). The relationship between  $\delta^{13}\text{C}$  and foot color also differed between colonies, but the interaction was only marginally significant (Table 2). In San Jorge, males with greener foot color had lower  $\delta^{13}\text{C}$  and presumably more pelagic diets compared to duller-colored males. Males from San Pedro showed a similar, but weaker negative trend, whereas no relationship between foot color and diet was evident in Marietas (Fig. 1d-f).



**Fig. 2** (a) Locations of focal brown booby colonies and a bathymetric map of the Pacific coast of México and Gulf of California. (b)–(e) Maps of each colony displaying tracks from all males during the chick-rearing period and the core foraging locations used by the greenest-skinned males (50% kernels of the greenest (top 50%) birds).

Core foraging locations are only shown when a colony's ornament (foot or gular skin) was significantly related to GPS tracking parameters (as reported in Table 1); silhouettes in upper right-hand corners designate ornament type. Bathymetric map from Amante and Eakins 2009



**Table 2** The relationship between diet (measured through blood plasma  $\delta^{13}\text{C}$ ) and gular and foot color of male brown boobies, analyzed via linear models

Variables	Gular color				Foot color			
	<i>F</i>	<i>p</i>	$\beta \pm \text{SE}$	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	$\beta \pm \text{SE}$	<i>R</i> <sup>2</sup>
$\delta^{13}\text{C}$	2.25	0.14			3.07	0.09		
Colony	0.02	0.97			0.36	0.69		
$\delta^{13}\text{C} * \text{Colony}$	<b>4.74</b>	<b>0.01</b>		<b>0.24</b>	<b>2.97</b>	<b>0.063</b>		<b>0.21</b>
Isla de San Jorge			<b><math>0.83 \pm 0.34</math></b>				<b><math>-1.39 \pm 0.56</math></b>	
Isla San Pedro Mártir			$-0.36 \pm 0.25$				$-0.34 \pm 0.25$	
Islas Marietas			<b><math>-0.69 \pm 0.26</math></b>				$0.03 \pm 0.24$	

Analysis of variance results and slopes  $\pm$  standard error (SE) of adjusted curves are shown for three breeding colonies: Isla de San Jorge, Isla San Pedro Mártir and Islas Marietas. Significant effects are shown in bold, and *R*<sup>2</sup> is shown for final significant models. Skin color and  $\delta^{13}\text{C}$  were standardized within colony prior to analysis (refer to “Methods” section for details)

## Skin color and foraging behavior

In further support of our prediction, the link between gular color and some foraging behaviors varied between brown booby colonies. Core foraging locations of the top 50% greenest-skinned males were predominantly coastal (with some pelagic offshore locations) for males nesting on San Pedro, whereas the greenest males in Marietas utilized both coastal and oceanic waters beyond the continental shelf (Fig. 1c-e). Our linear models indicate that mean distance of foraging locations to the coast and the mean trip duration impacted gular skin color differently on the three colonies (significant foraging\*colony interactions in Table 3). Males showed the strongest link between mean distance from the coast and gular color on San Pedro (in the mid-Gulf of California), where greener-skinned males foraged significantly closer to the coast than their duller-colored counterparts (Table 3, Fig. 3b). On Marietas (our most southern site), male brown boobies showed a marginally significant relationship between gular skin color and the distance of foraging locations to the coast ( $p=0.07$ ); the greenest-skinned males were those with more offshore foraging (Table 3, Fig. 3c). No relationship was apparent between distance from coast of foraging locations and gular coloration on San Jorge (Table 3, Fig. 3a). Males with greener gulars performed longer trips compared to less green males on Marietas, but mean trip duration was not strongly associated to males' gular skin coloration in San Pedro or San Jorge (Table 3). The links between mean ocean depth while foraging and gular color and mean flight distance and gular color did not differ between colonies (Table 3).

The relationships between foraging metrics and foot color did not differ between colonies (all interactions, foraging behavior \* colony, were non-significant; Table 3). However, greener-footed males on San Pedro foraged significantly closer to shore compared to less green males, echoing the relationship between gular skin and distance from coast on this island (Table 3, Fig. 3e).

## Discussion

Many studies assume that ornamental traits are conserved within a species. Indeed, in our investigation of a marine predator, the brown booby, carotenoid-dependent skin color was reflective of foraging behavior and/or diet on each of our three colonies. However, the colonies varied in which trait (foot versus gular skin color) was associated with foraging metrics, as well as in which foraging attributes were linked to carotenoid-rich ornaments. For example, greener gular skin was associated with longer trips to access pelagic prey where foraging habitat was deep (Marietas colony) versus a benthic diet where foraging habitat was relatively shallow (San Jorge colony). Our models testing the links between skin color and foraging/diet explained a significant but small proportion of the variance in our data ( $R^2=0.14-0.24$ ), suggesting that other factors not measured in our study influence these relationships (e.g., nutritional composition of diet or age-related variation in skin color and foraging habits; Torres and Velando 2010). However, the geographical differences found illustrate a consistent but flexible link between diet and ornamentation, a link that may echo variation in locally optimized diet and foraging behavior. More broadly, our results emphasize that even geographically proximate populations can differ in their ornamental traits.

Below, we discuss the likely effects of foraging and display environment on the foraging-ornament link (sections a and b, respectively) and our main conclusions (section c).

### (a) The influence of foraging environment on the foraging-ornament link

In our study, plasma  $\delta^{13}\text{C}$  was the explanatory variable most consistently related to brown booby skin color and the variable with the most distinct geographic patterns. Specifically, beta values relating  $\delta^{13}\text{C}$  to both gular and foot skin showed latitudinal clines (Table 2)—a finding that can be interpreted in terms of benthic versus pelagic prey

**Table 3** The relationship between foraging behavior and gular and foot color of male brown boobies, analyzed via linear models

Variables	Gular skin				Foot skin			
	<i>F</i>	<i>p</i>	$\beta \pm SE$	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	$\beta \pm SE$	<i>R</i> <sup>2</sup>
Distance to the coast (km)	2.14	0.14			2.73	0.10		
Colony	0.002	0.99			0.07	0.93		
Distance from coast*Colony	<b>4.14</b>	<b>0.02</b>		<b>0.14</b>	1.43	0.24		
Isla de San Jorge			$-0.21 \pm 0.28$				$0.29 \pm 0.42$	
Isla San Pedro Mártir			<b><math>-0.36 \pm 0.14</math></b>				<b><math>-0.29 \pm 0.13</math></b>	
Islas Marietas			$0.42 \pm 0.23$				$0.05 \pm 0.21$	
Depth (m)	0.02	0.88			0.41	0.52		
Colony	0.01	0.98			0.32	0.73		
Depth*Colony	1.80	0.17			0.03	0.96		
Isla de San Jorge			$0.22 \pm 0.26$				$-0.06 \pm 0.51$	
Isla San Pedro Mártir			$0-10 \pm 0.15$				$-0.11 \pm 0.14$	
Islas Marietas			$-0.38 \pm 0.24$				$-0.04 \pm 0.23$	
Trip duration (h)	1.22	0.27			0.27	0.60		
Colony	0.06	0.94			0.30	0.74		
Trip duration *Colony	<b>5.51</b>	<b>0.006</b>		<b>0.16</b>	0.03	0.97		
Isla de San Jorge			$0.16 \pm 0.48$				$0.04 \pm 0.55$	
Isla San Pedro Mártir			$-0.02 \pm 0.14$				$0.07 \pm 0.14$	
Islas Marietas			<b><math>1.27 \pm 0.36</math></b>				$0.16 \pm 0.37$	
Total flight distance (km)	1.41	0.23			0.48	0.49		
Colony	0.04	0.96			0.29	0.75		
Flight distance *Colony	2.81	0.067			0.01	0.98		
Isla de San Jorge			$0.07 \pm 0.37$				$0.02 \pm 0.41$	
Isla San Pedro Mártir			$-0.005 \pm 0.14$				$0.10 \pm 0.14$	
Islas Marietas			<b><math>0.76 \pm 0.29</math></b>				$0.05 \pm 0.28$	

Analysis of variance results and slopes  $\pm$  standard errors (SE) of adjusted curves are shown for three breeding colonies: Isla de San Jorge, Isla San Pedro Mártir and Islas Marietas. Significant effects are shown in bold, and *R*<sup>2</sup> is shown for final significant models, only. All foraging variables were standardized within colony prior to analysis

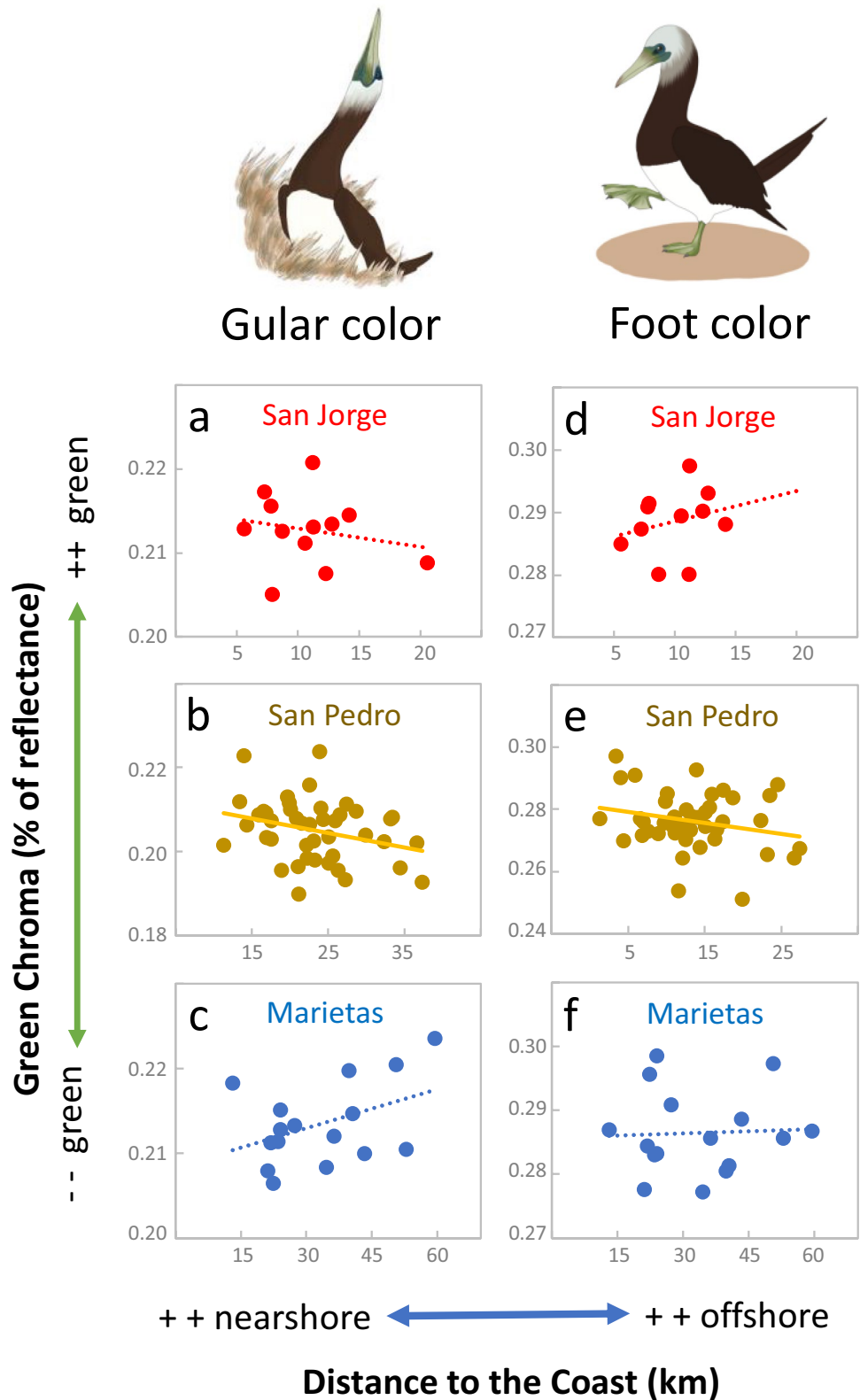
consumption (Michael et al. 2018). For gular skin, our data show a shift from a benthic prey-green skin association in the shallow waters in the north (San Jorge) to a similar, but non-significant association in the mid-Gulf (San Pedro), to a pelagic prey-green skin association in the deepest waters to the south (Marietas; Fig. 1a-c). In contrast, our foot skin models show a strong pelagic prey-green skin association in the north (San Jorge) and the relationship between plasma  $\delta^{13}\text{C}$  and foot color weakening and disappearing to the south (Table 2, Fig. 1d-f).

It is unsurprising that a pelagic diet is sometimes linked to greener, more carotenoid-rich skin ornaments in brown boobies. This finding is consistent with the observation that phytoplankton, and by extension, phytoplankton-based pelagic food webs likely have higher concentrations of carotenoids necessary for brown booby ornamentation (e.g., zeaxanthin) compared with the benthic algae and benthic algae-based food webs (Bonilla et al. 2005; Michael et al. 2018; Montoya et al. 2018). The pelagic diet-green skin association is also consistent with our previous study of

brown boobies on Marietas during the non-breeding period and courtship phase (Michael et al. 2018). In addition, previous studies stress the prevalence and high nutritional value of northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) – two pelagic fish – in the diet of brown boobies in the Gulf of California and nearby regions (Mellink et al. 2001; Castillo-Guerrero et al. 2016). These important prey species are available to birds at all three of our focal colonies.

The association between benthic prey consumption and green gular skin on San Jorge is unique within our study. It is the only case where benthic prey are linked to more carotenoid-rich skin coloration. Notably, benthic fish are more prevalent and diverse around San Jorge than near Marietas or San Pedro (Mellink et al. 2001), and previous authors proposed that this reliable and abundant source of benthic fish makes San Jorge an especially successful breeding site for brown boobies (Castillo-Guerrero et al. 2016). Benthic algae (and by extension, benthic fish) likely contain a greater diversity of carotenoid pigments but in lower concentrations

**Fig. 3** The relationship between male brown booby gular or foot color and distance to the coast while foraging in three colonies nesting at Isla de San Jorge (**a**, **d**), Isla San Pedro Mártir (**b**, **e**), and Islas Marietas (**c**, **f**). Standardized values of all variables were used in independent linear models. Solid adjusted regression lines indicate slopes significantly different from zero. Brown booby males display carotenoid dependent gular color during sky-pointing display and foot skin color during parading. Artwork by Nathan Michael



compared with phytoplankton (and pelagic fish) (Bianchi et al. 1997; Bonilla et al. 2005). Our data suggest that San Jorge males generate high-quality gular ornaments using

pigments sourced from locally abundant benthic prey. Potentially, the San Jorge colony represents a unique location where higher-quality gular ornaments are not driven by



reliance on a few carotenoid-rich pelagic prey species, but instead, result from a wide array of benthic prey and carotenoids ultimately derived from benthic algae.

One puzzling aspect of our results is the seeming contradiction on San Jorge, where greener gular skin in male brown boobies is associated with a benthic diet (higher  $\delta^{13}\text{C}$  values), but greener foot skin is associated with a pelagic diet (lower  $\delta^{13}\text{C}$  values). One possible explanation is that different types of carotenoids are deposited in these two skin regions: presumably more abundant pelagic prey-derived carotenoids in the larger foot skin region, and presumably rarer benthic carotenoids in the smaller gular skin region. Together, these two traits may provide females with a more complete picture of male diet and foraging success than one trait alone. Another potential explanation is that females rely on the two skin traits at different times, for example in Pacific sardine and northern anchovy-abundant periods versus sardine and anchovy-depauperate periods when benthic prey could be more critical to breeding success. Further studies could help explain why opposing skin color-dietary relationships exist within a single population.

Beyond the association of ornamental traits with  $\delta^{13}\text{C}$ , our study uncovered colony-specific associations in brown boobies between (1) greener gular skin and both foraging trip duration and total flight distance (Marietas only), and (2) greener gular and foot skin and distance to coast (San Pedro only). These associations likely reflect the unique geography and spatial distribution of prey around Marietas and San Pedro. For example, Marietas birds used core foraging regions in both coastal and pelagic locations (Fig. 2e). As in other seabirds (Weimerskirch et al. 1997; Weimerskirch 1998), shorter trips (here to coastal foraging sites) may be important for brown booby chick-provisioning, and longer trips (here, to pelagic regions), more critical for adult self-care. Marietas males making longer mean foraging trips (taking more time and covering greater distances) may consume more carotenoid-rich pelagic prey. The greater time and distance required to access core pelagic foraging sites may pose a cost for breeding males to acquire carotenoid-rich skin color. In contrast, San Pedro birds forage along known anchovy spawning zones: the transition zones of 200–2000 m depth on either side of the Gulf of California, south of San Pedro, and between the islands Tiburón and Ángel de la Guarda to the north (Fig. 2c-d) (Green-Ruiz and Hinojosa-Corona 1997). These transitional depths may be ideal for accessing anchovies and other pelagic fish such as sardines because fish are forced to slightly shallower areas where they are more accessible to diving seabirds. Near San Pedro, transitional depths are often close to the coast and this geography may drive the significant relationship we observed between distance to coast and the color of both skin traits. Specifically, highly skilled foragers may outcompete other boobies in the most productive anchovy foraging

zones (near the coast), forcing less skilled foragers to more offshore areas (Fig. 3, Table 3). Indeed, San Pedro supports one of the largest brown booby colonies in the world (Lluch-Cota et al. 2007), so its resident males likely experience strong intraspecific competition, a generally powerful influence on seabird foraging dynamics (Birt et al. 1987; Ballance et al. 1997).

Carotenoid-dependent color traits rely heavily upon the availability of carotenoids in the environment and the diet (e.g. Velando et al. 2006; Hill et al. 2009), particularly in species that deposit unmodified dietary carotenoids (e.g., zeaxanthin and lutein) into the integuments (McGraw 2006). However, the expression of these color traits is also influenced by the uptake of other essential nutrients such as dietary fats, lipids, and proteins (Peneaux et al. 2021a for a review). For instance, dietary fats contribute to carotenoid pigment absorption and transport via lipoproteins, whereas proteins (keratin) play a key role in forming the collagen fibers upon which pigments are deposited in the skin (Shawkey and Hill 2005; Peneaux et al. 2021a). Experimental evidence where food and carotenoids have been manipulated indicates that overall nutrition influences color expression (Hill et al. 2009; Pérez-Rodríguez and Viñuela 2008), and in some species, birds are capable of selecting carotenoid-rich foods (Senar et al. 2010; Walker et al. 2014), or a combination of carotenoids and particular macronutrients (lipids) that enhance ornamental color (Peneaux et al. 2021b). In the brown booby, it is possible that differences among colonies in the specific combinations of macronutrients and carotenoids that birds obtain in their diets may contribute to locally optimized ornamental gular and foot color and may explain the differences we found among colonies in the link between diet and green coloration (Peneaux et al. 2021b). This hypothesis should be tested in future studies.

### **(b) The influence of display environment and environmental severity on the foraging-ornament link**

Sexual traits are simultaneously under ecological and sexual selection, which may result in geographic variation in the strength and direction of selection and variation in the mean sexual phenotype (Cornwallis and Uller 2010). Our data suggest that brown boobies vary geographically in terms of the trait used as their primary carotenoid ornament (gular versus foot skin) or at least, the ornament that is associated with diet and foraging behavior. Gular and foot color is related to diet on San Jorge and to foraging behavior on San Pedro, while gular color (but not foot color) is related to both diet and foraging behavior on Marietas. Notably, ornamental traits are unlikely to be conserved in the genus *Sula*, as previous research on Marietas brown boobies established gular skin color's link to foraging, parental care, and chick quality,

but foot skin color has been associated with reproductive investment in the closely related blue-footed booby (Torres and Velando 2003; Montoya and Torres 2015; Michael et al. 2018).

Environmental variation may induce changes in the target of sexual selection or the amount of investment in ornaments. Within the brown booby, local display environments and signal efficacy may partially determine which trait is used as a primary ornament. Indeed, environment has been shown to alter how signals are received and the type of signal or ornament generated by the sender (Gomez and Théry 2004; Stuart-Fox and Ord 2004). Islas Marietas, the southernmost colony of our study, is a densely grass-covered island. Here, gular ornament quality is clearly linked to foraging parameters and gular skin is likely the most visible signal to females, with sky-pointing behaviors conspicuously advertising this trait, while feet are often concealed by the dense grass (as illustrated in Figs. 1, 3). Indeed, parading behavior (i.e., exaggerated form of ordinary wading) associated with the display of foot ornaments is relatively rare on Marietas (R. Torres, personal observations). To the north, San Pedro and San Jorge are covered with sand and rock and almost devoid of leafy vegetation. In such locations, feet can be prominently displayed through parading behaviors, and foot ornaments may be at their highest signaling efficacy without vegetation to obscure them. On San Pedro, male brown boobies perform both sky pointing and parading (Friesen and Anderson 1997). As both foot and gular color are linked to foraging behaviors on San Pedro and diet in San Jorge, we predict that on these two colonies (but not in Marietas), both foot and gular skin color play an important role in mate choice.

Changes in ornamentation, for instance the size of the trait, can also occur when viability selection associated with investment in the ornament varies among environments (Kokko 1998; Candolin and Heuschele 2008). Sexual selection theory suggests that severe environmental conditions drive ornamentation to be more conservative (Kokko 1998). Greater exposure to El Niño Seasonal Oscillation and lower mean ocean productivity (Escalante et al. 2013), coupled with higher rates of predation and kleptoparasitism from other seabirds may create harsher conditions on Marietas relative to more northern colonies, resulting in lower breeding success (Cornejo-Ortega et al. 2016). These challenges likely limit the energy available to invest in large ornaments such as the feet, making the gular patch a more conservative way to communicate parental ability, while not overextending individual birds' health.

### (c) Conclusions

Our study supports the hypothesis that carotenoid ornament quality varies in response to diet and foraging

tendencies in free-ranging predators. Moreover, our study supports the hypothesis that this relationship is variable among populations, such that carotenoid-rich ornaments might reflect locally optimized foraging behaviors and diets. We predict that the spatially variable link between carotenoid coloration and foraging behavior and diet that we observed in the brown booby may be widespread in species utilizing dietary carotenoid pigments for sexual displays, especially in species with bi-parental care. Most broadly, our results stress that in studies of sexual ornaments, perhaps especially carotenoid-dependent ornaments, we cannot assume ornaments or ornament signal content are ubiquitous within species, even when ornaments appear similar among populations.

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### Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** All applicable international, national, and institutional guidelines for the care and use of animals were followed. Permissions to conduct the study were granted by Secretaría de Medio Ambiente y Recursos Naturales and Consejo Nacional de Areas Naturales Protegidas (SGPA/DGVS 04708–16, 011542–17). The study was approved by the University of Akron's Institutional Animal Care and Use Committee (Protocol 16–06-13-WBC). This work was supported by National Geographic (WW-056R-17), the Universidad Nacional Autónoma de México (PAPIIT-IN211017), and the University of Akron. J. Adams

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