WING MORPHOLOGY AND FORAGING ECOLOGY OF PACIFIC BOOBIES: ECOMORPHOLOGY AND CHARACTER DISPLACEMENT

A Thesis submitted in partial fulfillment of the requirements

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By

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Abstract

**WING MORPHOLOGY AND FORAGING ECOLOGY OF PACIFIC BOOBIES: ECOMORPHOLOGY AND CHARACTER DISPLACEMENT**

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Wing and beak morphology are key components of the functional design of birds, and therefore an important determinant of their foraging ecology. This is especially the case for seabirds that traverse great distances in search of prey. Wing size and shape, expressed as wing loading and aspect ratio respectively, are parameters that can unveil differences and help understand the ecology of seabirds. Six species of boobies inhabit the Pacific, and five of them are the focus of this study: three pelagic species, the Masked (*Sula dactylatra*), Red-footed (*S. sula*), Brown (*S. leucogaster*), and two coastal species, Blue-footed (*S. nebouxii*) and Peruvian (*S. variegata*) Booby. They differ in their distribution (coastal vs. pelagic) and degree of overlap (sympatric vs. allopatric), and therefore were predicted to manifest differences in their wing and beak morphologies. Two of the most abundant species of seabirds along the South American coast are the Peruvian and the Blue-footed Booby. Although these species are largely allopatric, they overlap in northern Peru. Sympatric species exploit similar resources and consequently competition is likely to arise between them, resulting in the potential for character displacement in their sympatric range. Therefore, these two species would be predicted to exploit slightly different niches and foraging strategies that would be manifested in wing and beak morphology.

The pelagic boobies showed ecological segregation among species and they differed in wing morphology from the two coastal boobies. Coastal boobies, on the other hand, showed evidence of character displacement in their wing morphology and body size, which suggests that competition plays an important role in their sympatric range. This study helps in our understanding of ecological interactions among Pacific boobies and how selective pressures have shaped the ecomorphology of these seabirds in different ecosystems.
Introduction

Birds have a remarkable range of behavioral, morphological, and physiological adaptations that have allowed them to inhabit a variety of environments. Wing and beak morphology are key components of their functional design and therefore are important determinants of their foraging ecology and breeding success. Seabirds in particular have to deal with high degrees of prey patchiness and seasonality in the marine environment, in addition to regional or local environmental features (Hunt & Schneider 1987).

Many seabirds exploit distant foraging grounds (Ashmole 1971) and use complex movement patterns and flight strategies to minimize energy expenditure (Schreiber & Burger 2002, Weimerskirch 2007, Philips et al. 2009, Troup et al. 2009). Wandering Albatrosses (*Diomedea exulans*) travel 10 to 1,000 km on their foraging trips using wind currents and optimal pathways to minimize energy expenditure. These long flights are characteristic when commuting from the colony to foraging patches or between patches (Fritz et al. 2003). Southern Royal Albatrosses (*Diomedea epomophora*) make shifts in flight modes using a commute-forage-commute strategy, varying their flight speeds according to wind conditions allowing them to travel distances ranging from 180 to 800 km (Troup et al. 2009). Magnificent Frigatebirds (*Fregata magnificens*) take advantage of wind energy generated by thermals to travel up to 200 km per foraging trip and reach altitudes of more than 2 km (Weimerskirch et al. 2003). Sooty Shearwaters (*Puffinus griseus*) have been shown to travel about 10,000 km from the coast of California to New Zealand while foraging throughout the Pacific Ocean using headwinds and crosswinds to save energy (Adams & Flora 2010). Hawaiian Petrels (*Pterodroma sandwichensis*) make trips of about 100 km per foraging trip with a body mass less than 0.5 kg (Adams & Flora 2010).

Seabirds show several wing adaptations that optimize locomotion while foraging (Pennicuick 1987, Shealer 2002, Brewer & Hertel 2007). Generally all seabirds share common morphological traits that reflect their adaptations to the marine environment: waterproofed feathers, streamlined shape, strong beaks, and webbed feet. Additional features that reflect their ecological diversity include wing size and shape. Wing loading is a measure of wing size that indicates the total weight borne by the wing; therefore birds with a high wing loading tend to have relatively small wings. Aspect ratio is a dimensionless index of the shape of the wing. Aspect ratio together with wing loading can help to better understand functional design and ecological interactions in seabirds (Spear & Ainley 1997, Hertel & Ballance 1999, Brewer & Hertel 2007).
The diversity of wing morphologies in birds is explained by a tradeoff between stability during flight and the ability to maneuver or control their flight. Flight requires a dynamic and changing airfoil, which can be observed in the continuous changes in their wing angles and/or shape (Thomas & Taylor 2001). The three-dimensional characteristics of a wing incorporate several factors, such as cord length, thickness, and curvature (also described as camber) that will affect performance. Additionally, changes in the angle of attack of the wing will affect the abilities of a flying animal to perform in different habitats and display different behaviors. Therefore, more subtle differences in the two-dimensional area of a wing (planform) could also describe differences in morphology and correlate with ecological niches in flying birds. More aft-swept wings (oriented backwards) at the distal end, and greater curvature at the mid wing are features known to increase lift, stability, and efficiency during sustained flight (Burkett, 1989; van Dam et al., 1991a,b, Lockwood et al. 1998, Brewer & Hertel 2007).

Most seabirds have long narrow wings (high aspect ratio) and large body masses relative to the size of their wings (high wing loading) that allow them to travel over long distances and adapt to wind changes over the ocean surface by maximizing gliding or dynamic soaring (Savile 1957). Starting from a general seabird wing with both high aspect ratio and wing loading (e.g., a gull), it is possible to observe the diverse specializations of shapes and sizes of seabird wings. Several configurations that depart from this general seabird form are described by Pennycuick (1987), such as the extremely long and narrow wings of a pelican or albatross (greatly adapted for dynamic soaring using the winds over the ocean's surface to reduce energy expenditure in flapping), the short, stout wings of a cormorant (a reflection of their diving habits and poor flying capabilities), or the extremely short narrow wings of auks or penguins (whose wings are reduced to increase powerful flapping underwater).

Birds and other flying organisms have adapted a variety of flight strategies, reflected in different flight modes and speeds, and often show a strong correlation between wing morphology, habitat, and/or behavioral specializations. Consequently ecological segregation in sympatric species is common and often observed in morphological features, including wing morphology. Brewer and Hertel (2007) found that sympatric Pelecaniformes showed differences in wing morphology that correlated with their specialized foraging strategies. For example, faster more pelagic flyers (e.g., boobies) showed higher aspect ratio and wing loading, whereas slower more maneuverable flyers, such as the Magnificent Frigatebird, had lower wing loading and aspect ratio. These morphological differences could reflect ecological segregation especially when resources are limited, during breeding seasons or chick provisioning, or with reduction of intraspecific competition during the breeding seasons in

Wing morphology and ecological adaptations have been studied in different taxa (bats: Norberg 1994, ground finches: Vanhooydonck et al. 2009, seabirds: Hertel & Ballance 1999, Brewer & Hertel 2007) showing how species segregate by flight speeds according to aspect ratio and wing loading; low aspect ratio and wing loading correlate with slower flying speeds and more maneuverable species, whereas high aspect ratio wings and high wing loading are often found in fast flyers that inhabit open areas. Flight speeds show strong correlations with wing morphology using different approaches that include simple measurements to more complex shape analyses (Norberg 1994, Birch 1997, Hixon et al. 2012). Differences in wing and beak morphology ultimately allow sympatric species or sexes within the same species to exploit resources in different ways, which reduces competition and optimizes energy efficiency (Brewer & Hertel 2007).

It is expected that sympatric species would potentially develop different functional designs in their wings and beaks, compared to the sites where they are allopatric, which could be reflected in their foraging strategies as well (Pennicuick 1987, Ballance et al. 1997). This phenomenon, known as character displacement, occurs when two or more sympatric closely related species with similar phenotypes (or traits) compete for similar resources (Dayan & Simberloff 1994, Schluter 2000, Grant & Grant 2006). Selection would then likely favor a different phenotype to exploit new resources and reduce competition. Schluter (2000) observed that evidence supporting ecological character displacement is abundant, mainly in morphological patterns. A common pattern is exaggerated divergence when species are in sympatry (i.e., phenotypic differences are greater where the species coexist than where they occur separately). A second pattern is the over dispersion of trait means (or constant size ratios), where phenotypes in ecologically similar species tend to be spaced evenly throughout a size axis or other phenotypic trait. Less frequently "species-for-species matching" may be observed, which could be understood as functional convergence or phenotype distributions between species that have evolved independently. Although character displacement has been reported in mammals (Dayan & Simberloff 1994), birds (Grant & Grant 2006, Reifová et al. 2011), reptiles (Losos 1990) and other taxa (Brown & Wilson 1956, Schluter & McPhail 1992, Saloniemi 1993), recently developed statistical models and more complex analyses have put some results under scrutiny (Dayan & Simberlof 2005, Goldberg & Lande 2006, Adams & Collyer 2007, Meiri et al. 2011).
Latitudinal gradients in morphological and other traits have been reported in birds and other vertebrates as a consequence of ecogeographical adaptations to climate patterns and diversity along these gradients (Alho et al. 2001, Phillimore et al. 2007, Gaston et al. 2008). Allen's and Bergmann's rules propose that appendage length decreases and body size increases, respectively, at higher latitudes as a result of less energetic constraints from the environment. One such case is distributions along latitudinal gradients where higher temperatures are often common towards the equator. Thus, a phenotypic gradient is often seen in populations that have wide latitudinal distributions. It is therefore important to describe the morphology of a species throughout its range and with enough replication to discard potential environmental effects.

Boobies and Gannets are a cosmopolitan family (Sulidae) of marine seabirds that forage and breed in both pelagic and coastal environments, and are noted for their spectacular plunge diving habits. Sulids possess long serrated beaks adapted to catch fish underwater and lack nostrils that prevent water from entering the breathing passages. Reversed sexual dimorphism in body size is generally strong in boobies, females being larger than males, but gannets show no dimorphism. Sulids have high aspect ratio wings (long and narrow) and somewhat pointed, well adapted for long sustained flight and plunge diving. In general, sulids lack maneuverability during flight due to their long wings, but some species such as the Red-footed Booby (Sula sula) and the Abbott's Booby (Sula abboti) nest in trees, which selects for more maneuverable wing designs. Unlike many other seabirds, sulids continuously molt their feathers and lack brood patches, both features that allow them to keep a constant streamlined shape while flying (Nelson 1978, del Hoyo et al. 1992).

Boobies differ in their distribution in the Pacific Ocean with some species being mainly coastal and near shore, and strongly associated with upwelling coastal habitats (Zavalaga et al. 2007). Other species are more pelagic, differing in their foraging strategies as well. Although plunge diving is the main foraging strategy, some species have developed aerial pursuit techniques, such as the Red-footed Booby (Ballance 1995). Exclusive plunge diving species enter the water from a variety of heights and angles, reaching different depths. This allows plunge divers to catch different prey along the water column and they are highly dependent on flight to capture and search for prey (del Hoyo et al. 1992). Thus, differences in foraging strategies and ecological niches among boobies are predicted to be manifested in their wing and beak morphology such that more tropical and generalist species would have larger beaks allowing them to forage on a wider variety of prey. More pelagic species should show higher wing loading and aspect radio, which is advantageous for longer offshore flights.
Six species of boobies inhabit the Pacific and are the focus of this study. The Masked Booby (*Sula dactylatra*) and Nazca Booby (*Sula granti*) have been recognized as two distinct species within the last 20 years as a result of morphologic, genetic, and geographical features (Pitman & Jehl 1998, Friesen *et al.* 2002). These two are the largest boobies and are highly pelagic, feeding farther from their nesting/roosting islands. They feed mainly on schooling fish and frequent deeper waters, taking larger prey than other boobies (del Hoyo *et al.* 1992). Masked and Nazca Boobies often travel 1,000-3,000 km from their nesting sites during non-breeding seasons (Huyvaert & Anderson 2004, cited in Steeves *et al.* 2005). The Red-footed Booby (*Sula sula*) is the smallest sulid and is considered highly pelagic. It preys mainly on flying fish and squid that have been chased out of the water by other predators. They are highly maneuverable, use aerial pursuit to hunt, and nest in tree tops (all others nest on the ground), making them the most versatile fliers of the group (del Hoyo *et al.* 1992, Ballance 1995, Weimerskirch *et al.* 2005, Weimerskirch *et al.* 2006). The Brown Booby is intermediate in size, and feeds mostly inshore on sardines and anchovies, but also on flying fish, squid, mullets, and other small fish when anchovies are scarce (del Hoyo *et al.* 1992, Mellink *et al.* 2001, Weimerskirch *et al.* 2009). These four sulids (Masked, Nazca, Red-footed, and Brown Boobies) are the most pelagic among the group.

The Peruvian Booby (*Sula variegata*) and the Blue-footed Booby (*Sula nebouxii*) are two of the most abundant seabirds in the eastern Pacific, mainly distributed along the South and Central American Pacific coast. Although some breeding colonies of Blue-footed Boobies also inhabit the Galapagos, they commonly breed on coastal islands and are strongly associated with nearshore habitats where upwelling is stronger and cool nutrient rich waters sustain high levels of primary productivity (del Hoyo *et al.* 1992). The Pacific Ocean off Peru and Chile is subject to some of the strongest upwelling conditions on the planet as a result of the cold and persistent Humboldt Current that sustains high biomasses of schooling fish, mainly Peruvian Anchovy (*Engraulis ringes*). This region is considered one of the most productive marine ecosystems and sustains large industrial and artisanal fisheries (Aranda 2009). Intensive fishing activities occur almost year round in both Chile and especially in Peru, where Peruvian Anchovies are the main resource for both marine organisms and fisheries. Therefore seabirds in this system, especially the Peruvian Booby that mainly feeds on Peruvian Anchovy, have to deal with both high levels of interspecific competition from other anchovy predators and competition with fisheries that capture about 8 million tons of Peruvian Anchovies every year.
Peruvian Boobies range from central Chile to northern Peru, whereas the Blue-footed Boobies are found from northern Peru to Mexico. Although these species show primarily an allopatric distribution, they overlap on several islands in northern Peru. As mentioned previously, sympatric species, such as these boobies in northern Peru, might experience resource overlap and consequently competition could arise between them. They would be predicted to exploit slightly different niches and foraging strategies that would allow them to coexist sympatrically in northern Peru. Therefore, these coastal boobies in the eastern Pacific are a good model to explore morphological character displacement in two closely related species (sister taxa), because they exploit similar environments and foraging strategies.

My research aims to compare body mass and wing morphology of four pelagic species (Masked, Red-footed, and Brown) with two coastal species (Peruvian and Blue-footed) of Pacific boobies in relation to their foraging strategies. I hypothesized that pelagic boobies would show higher aspect ratios and wing loadings, more aft-swept distal wings, and more curved mid wings, which are adaptive for long sustained flights that increase stability, speed, and efficiency. Alternatively, coastal boobies would show lower aspect ratio and wing loading, and straighter wings. I also aimed to explore the potential for character displacement in beak and wing morphology between the two coastal boobies (Peruvian and Blue-footed) at their site of sympatry in northern Peru. I predict that Blue-footed Boobies would show larger beaks (allowing them to catch a greater variety of prey), higher aspect ratio and wing loading, more aft-swept wings, and curved mid wings, all related to their slightly more pelagic habits.
Methods

Study Sites

Boobies were captured and sampled on coastal islands along the eastern Pacific (Fig. 1) while sitting near their nests or courting during the breeding season. Peruvian Boobies were sampled off the coast of Chile at Pajaros Island (29° 54’ S, 71° 51’ W), Peru at Mazorca Island (11° 23’ S, 77°44’ W), and Lobos de Tierra (6° 25’ S, 80° 51’ W). Blue-footed Boobies were sampled off the coast of Peru on Lobos de Tierra Island and in Mexico on El Rancho Island (25° 09’ N - 108° 22’W). Lobos de Tierra Island is the sympatric region for these species (Fig.1).

Data collection

At each locality, 26 birds of each species were captured (13 males and 13 females, except Peruvian Boobies in Lobos de Tierra where 14 males and 12 females were captured) and were later released unharmed after measurements were taken. Measurements included: body mass (g) using a spring scale (PESOLA ±10g); beak (from naso-frontal hinge to the tip) and total skull (head and beak) lengths, beak width and depth (height and width at the approximate site corresponding to the nares), using digital calipers (± 1 mm). One or more digital photographs of the fully outstretched wing and body of each individual were taken above perpendicularly with a 12 megapixel digital camera (Coolpix S570, Nikon Inc. Melville, NY). All photos included a ruler for calibration. Wing area and wing length were measured from the photos following the methods of Pennycuick (1989) and Brewer and Hertel (2007) using ImageJ 1.44p (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA 2012).
Wing length was measured as the linear distance from the sternum to the wing tip. Wing area was obtained from the partial wing area from each picture (Pennicuick 1989, Brewer and Hertel 2007), as shown in Figure 2v. This partial wing area was then doubled to obtain the total wing area.

These data were used to calculate wing loading and aspect ratio for each individual as follows:

**Aspect ratio:**

\[
\text{Wingspan}^2 = \frac{(2 \times \text{wing length})^2}{2 \times \text{partial wing area}} 
\]

**Wing loading:**

\[
\frac{\text{Weight}}{\text{Total area}} = \frac{\text{mass} \times (9.8 \text{m/s}^2)}{2 \times \text{partial area}} 
\]

Figure 2. Illustrations of measurements. i) head length, ii) beak length, iii) beak width, iv) beak depth and v) partial wing area.

Beak morphology among groups was compared using measurements of beak length (BKLN) and two indices of the beak, relative beak length (BKRL) and beak shape (BKSHP). BKRLN and BKSHP were calculated as follows:

**BKRLN:** relative beak length = \frac{\text{beak length}}{\text{head length}}.

Where: head length = skull length + beak length,

**BKSHP:** beak shape = \frac{\text{beak width}}{\text{beak depth}}.
Analyses

For all booby species (both pelagic and coastal), differences among parameters (body mass, aspect ratio, wing loading, and planform shape) were compared using one-way ANOVA and Tukey- HSD comparisons. For the two coastal species, differences among parameters (body mass, aspect ratio, wing loading, beak length, BKRL, and BKSHP) were compared considering sexes and species at each site using a Three-way Factorial ANOVA (with species (SP), sex (SEX), and site (SITE) as fixed factors); Tukey HSD comparisons were performed. Sites were considered as sympatric (SYM) for Lobos de Tierra Island and allopatric (ALLO) for Pajaros and Mazorca Islands for Peruvian Boobies, and El Rancho for Blue-footed Boobies. Significant SITE×SP interactions indicated changes in the sympatric site and potential character displacement. A second test was performed for all parameters with two-way ANOVAs; sexes were combined after finding no significant intraspecific differences or if intraspecific differences were less than interspecific differences.

Body mass and wing length for Peruvian Boobies in the allopatric and sympatric sites were tested for differences among the three islands (Pajaros, Mazorca, and Lobos de Tierra) using a One-Way ANOVA to detect a latitudinal gradient. There were no differences along its range (p>0.005). Therefore, grouping Pajaros and Mazorca Islands into one factor (ALLO) was feasible. All data were approximately normally distributed and homoscedastic so no transformations were performed. All tests were performed using SYSTAT 11 for Windows (SYSTAT Software Inc. 2004), with α=0.05.

Thin-plate spline/Relative warp analysis (TPS/RW) (Bookstein 1991) was used to detect more subtle changes in wing shape that may not be captured by aspect ratio. This method allows the geometry of a structure to be captured by using coordinates of points on the outline of an outstretched wing. These coordinates are known as landmarks whose positions are compared among specimens. Outlines of the wings were obtained for each specimen using ImageJ and landmarks were set along the wing using the tpsDIG 2.16 program (Rohlf 2010). The deformation generated by the variation of the positions of the landmarks among specimens was plotted in two dimensions. Sixty four equidistant landmarks were used to describe the shape of the wing as in Brewer and Hertel (2007). This method allows that points of comparison are all in the same relative position.

After landmarks were obtained, the TPS/RW analysis was run using the tpsRW 1.49 program (Rohlf, 2010). In this process wing size differences were standardized by reducing each wing configuration of landmarks to a centroid size of one, making the comparisons strictly on shape. A consensus wing was generated from the entire
sample through a superimposition analysis of generalized Procrustes (equivalent to least-squares estimates for translation and rotation parameters), and wings of each specimen were compared to this consensus wing.

Differences in the shape of the wings of each group to the consensus wings were captured by linear combinations called warps, which are analogous to principal components in a PCA. The greatest differences are manifested in the first warp, and the variation summarized in successive warps is orthogonally independent and accounts for the remaining variation of the sample set (Bookstein 1991). When overlaying each wing to the consensus wing, scores were generated and a vector-based output (magnitude and direction) represented how the landmarks for each group differed from the consensus. Each species was plotted in two dimensions using the first and second warps to visualize differences among species. Differences among groups in warp score values were detected using three-way and two-way factorial ANOVAs. Data from Red-footed, Masked, and Brown Boobies from Johnston Atoll collected previously by FH were used to compare differences between the coastal and pelagic boobies.
Results

Wing morphology in Pacific boobies: pelagic vs. coastal species

Body mass differed significantly among boobies (ANOVA: $F_{4,184}=75.01$, $p<0.001$); the two coastal boobies did not differ from each other, nor did the Masked (Fig. 3). Aspect ratio differed significantly among species (ANOVA: $F_{4,183}=20.95$, $p<0.001$). Peruvian Boobies had the lowest aspect ratio, whereas Masked Boobies the highest (Fig. 4). Wing loading also differed significantly among species (ANOVA: $F_{4,183}=61.8$, $p<0.001$). Peruvian, Blue-footed, and Masked Boobies had significantly high wing loading, whereas Red-footed Boobies had the significantly lowest wing loading, with Brown Boobies intermediate (Fig. 5).

A total of 124 warps was generated from the Relative Warp Analysis for all boobies, from which the first 2 warps described 75% of the total variance. Relative warp 1 described the distal wing and the notch at the base of the wing. Higher values represented less aft-swept wings with a notch, whereas lower values showed slightly aft-swept wings and a tapering at the wing base (Fig. 6). Peruvian and Blue-footed Boobies had straighter wings and a more pronounced notch compared to the three pelagic boobies (Fig. 7, ANOVA: $F_{4,181}=56.259$, $p<0.001$). Relative Warp 2 described the curvature on mid wing with higher values representing less curvature and lower values more curvature (Fig. 8). Brown Boobies had the most curved wing, and although Masked Boobies did not significantly differ from Brown Boobies, they along with the other boobies had somewhat less curved wings (Fig. 9, ANOVA: $F_{4,181}=4.87$, $p<0.001$).

Wing and beak morphology and character displacement in coastal Boobies

Body mass

Mean body mass for coastal boobies by sex and site are shown in Figure 11. There were significant differences in body mass between sexes, species, sites, and a significant species and site interaction (Table 1). Tukey’s HSD tests showed that females had a larger body mass than males (of their corresponding site) in all cases (12-26%). Male Peruvian Boobies showed no difference in body mass among all sites. Male Blue-footed Boobies differed between the allopatic and sympatric sites, but were similar to Peruvian Boobies. Female Peruvian Boobies in the sympatric site were similar to male Blue-footed Boobies in the same site. Blue-footed Booby females on the other hand were similar in both sites, but larger than all but female Peruvian Boobies in the allopatic site.
When grouping sexes there was a significant interaction between species and site (ANOVA: SP×SITE $F_{1,126}=5.322$, $p=0.023$). Tukey HSD test showed differences between Peruvian and Blue-footed Boobies only in the site of sympatry (Fig. 12).

**Beak Morphology**

Beak length differed among sites, sexes, and species and there was a significant interaction between species and site (SP×SITE) (Table 2). Female beak length was significantly larger (5-7%) than males in all cases (Tukey HSD $p<0.005$) and some segregation in beak length was observed in the sympatric site (Fig. 13). There were significant differences between species and sites when grouping sexes (ANOVA: SITE: $F_{1,126}=127.11$, $p<0.001$; SP: $F_{1,26}=8.022$, $p=0.005$). Peruvian Boobies in the sympatric site had slightly smaller beaks than other Peruvian Boobies and their beaks overall were significantly smaller than those of Blue-footed Boobies (Fig. 14).

There were significant overall differences in relative beak length between sexes, species, and sites and there was a significant interaction between species and site (SP×SITE) (Table 3). All females had larger beaks than males, although this difference was not significant (Fig. 13). Peruvian Boobies in the sympatric site had relatively smaller beaks than all other boobies (Fig. 15), and this pattern was the same when grouping sexes (Fig. 16, Table 4).

Beak shape index reflects the relative width of the beak. There were no significant differences between sexes or sites (Fig. 17), but a marginally significant difference between species (ANOVA: SP: $F_{1,122}=3.959$, $p=0.049$). There was a significant interaction between site and species (ANOVA: SP×SITE: $F_{1,122}=11.019$, $p=0.001$), which could be seen when grouping sexes (Fig. 18). Blue-footed Boobies in the allopatric site had significantly broader beaks than in any other locality, except Peruvian Boobies in the sympatric site (ANOVA: SP×SITE: $F_{1,126}=11.281$, $p=0.001$).

**Aspect ratio**

Blue-footed Boobies had a significantly higher aspect ratio than Peruvian Boobies (ANOVA: SP: $F_{1,122}=48.28$, $p<0.001$) and there were no differences between sexes, species, or sites. There was no significant interaction at any level in the three-way ANOVA. After grouping sexes, Blue-footed Boobies still had significantly higher aspect ratios than Peruvian Boobies (ANOVA: SP: $F_{1,126}=48.22$, $p<0.001$; Fig. 19).
Wing loading

Wing loading differed between sexes, species, and sites (Table 5, Fig. 20). There were significant interactions between species and site (SP×SITE) and site and sex (SEX×SITE). Differences in wing loading between sexes were found only in the allopatric sites (Pajaros and Mazorca, and El Rancho) (p < 0.05 for each pair). In the sympatric site (Lobos de Tierra), wing loading converged between sexes and between species.

When grouping sexes, wing loading for Blue-footed Boobies in allopatry was lowest as shown by the significant interaction of species and site (Fig. 21, ANOVA: SP×SITE: F₁,126=5.362, p=0.022), which is most likely an effect of the males in that locality.

Thin Plate Spine / Relative Warp Analysis

A total of 128 individuals were used to generate a consensus wing for all coastal boobies producing 124 relative warps. The first 4 warps explained 82% (53%, 12%, 10%, and 7%, respectively) of the variance in the sample. Subsequent warps explained about 3% or less of the variance and were not considered further.

Relative warp 1 explained the variation mainly at the distal wing as well as the wing base. Higher values showed less aft-swept wings (oriented slightly forward) and the converse for lower values (Fig. 22). ANOVA results showed a significant interaction of species and site (SP×SITE: F₁,120=4.152, p=0.044), and significant differences between species. Female Peruvian Boobies in the sympatric site had significantly higher values than male Blue-footed Boobies (Fig. 23).

Relative warp 2 focused on differences in the mid wing. Higher values represented a less curved and narrower mid wing, and lower values a broader mid wing with greater curvature (Fig. 24). There was a significant interaction between species and site (ANOVA: SP×SITE: F₁,120=11.577, p=0.001) and differences between sexes and between species (Fig. 25). These differences occurred only in the sympatric site, where Blue-footed Boobies showed a narrower mid wing than Peruvian Boobies. No difference was apparent between sexes in any site or species, and relative warp 2 values in the allopatric sites were similar.

Relative warp 3 described the transition from the mid wing to the distal wing (Fig. 26), where higher values showed broader wings in this transition site, and lower values represented slightly more curved and narrower and pointed wings. ANOVA results found significant differences between species where Peruvian Boobies showed a broader transition area than Blue-footed Boobies only in the site of sympatry (ANOVA: SP: F₁,120=26.736, p<0.001) (Fig. 27). No significant interactions were found.
Relative warp 4 focused on the transition between the wing base and the mid wing on the trailing edge. Higher values represented broader wings in the transition site, and lower values showed narrower wings with greater curvature in the trailing edge (Fig. 28). Overall significant differences were found between species, site, and sex, but no interaction between any factors was detected (Table 6). Peruvian Boobies had higher values showing broader less curved transition sites than Blue-footed Boobies. In the sympatric site both species showed lower values (not significant) than in their respective allopatric sites. Differences in the sympatric site were slightly reduced compared to the allopatric sites (Fig. 29).

When warps 1 and 2 values were displayed in an ordination plot, obvious differences in the sympatric site showed that Blue-footed Boobies (male and female) were more distant from Peruvian Boobies, especially females (Fig. 30). When grouping sexes, Relative Warp 1 showed no significant differences between species or sites. On the other hand, Relative warp 2 showed a significant interaction between species and site (SP×SITE), where Blue-footed Boobies in the sympatric site showed higher values than Peruvian Boobies (Fig. 31 and 32), but species did not differ in allopatry.
Discussion

Boobies are widely distributed in the Pacific, with the Masked, Brown, and Red-footed Boobies having a more pantropical distribution, whereas Blue-footed and Peruvian Boobies are found in the eastern Pacific (del Hoyo et al. 1992, Patterson et al. 2011). These distribution patterns have selected for sulids to adapt to a patchy, low resource tropical environment, but younger lineages have expanded to more highly nutrient-rich systems exploiting slightly different functional designs and foraging strategies. Body size differences among pelagic (Masked, Brown, and Red-footed) boobies suggest ecological segregation and reflect the different ways they exploit this patchy environment. Also, there were significant differences between these pelagic boobies and their coastal relatives in wing morphologies, with pelagic species generally being adapted to long and sustained flights.

A sulid phylogeny suggests that Blue-footed and Peruvian Boobies diverged from a common ancestor and now have a parapatric distribution in the Eastern Tropical Pacific (Friesen & Anderson 1997, Patterson et al. 2011) with a strong dependence on cold upwelling systems (Zavalaga et al. 2008, Taylor et al. 2011). Although both are described as coastal species, a subspecies of Blue-footed Booby also inhabits the Galapagos Islands (Sula nebouxii excisa, Tood 1948) and is somewhat more generalized compared to its eastern counterpart (Anderson 1989, Anderson & Ricklefs 1992, Castillo-Guerrero & Mellink 2007). This wider and more pantropical distribution of the Blue-footed Booby could indicate that they are more closely related to the ancestral condition than Peruvian Boobies, which is not as pelagic or tropical a species. Although differing somewhat in allopatry, there is evidence for character displacement in the site where these two species of boobies are sympatric suggesting that competition plays an important role in their ecology.

_Wing morphology in Pacific boobies: pelagic vs. coastal ecomorphs_

Although Pacific boobies generally share similar marine habitats (Savile 1957) and plunge diving behaviors, there were variations in wing morphology that reflect ecological differences. Wings in all boobies are long, narrow, and slightly pointed in comparison with other marine species as seen in the high aspect ratio values (Fig. 4) and planform wing configurations (Figs. 6 and 8). Morphological differences in pelagic boobies showed wings adapted for long flights, as would be expected by their foraging habits.
Aspect ratio among boobies differed significantly (Fig. 4) showing concurrent patterns with their behavior and foraging habitats. Peruvian Boobies had the lowest aspect ratio reflecting their strongly coastal habitat, reduced movements, and being strongly linked to the coastal upwelling in South America (Peru and Chile) compared to other boobies. Blue-footed Boobies had an intermediate aspect ratio and differed from the other coastal Peruvian Booby, possibly reflecting its slightly more pelagic habits in tropical or warmer areas. They also tend to have higher dispersal during breeding and non-breeding seasons and a greater prey size spectrum (Castillo-Guerrero & Mellink 2007, Ceyca & Mellink 2009) compared to the more coastal Peruvian Boobies. Masked Boobies had the highest aspect ratio and are highly pelagic. They perform long distance movements and non-breeding foraging flights of up to a thousand kilometers (Huyvaert & Anderson 2004, cited in Steeves et al. 2005).

Wing loading values closely matched the distribution of body masses for the pelagic boobies. Masked Boobies showed the highest wing loading, as expected from a highly pelagic species. Masked Boobies are the largest and known to the make the farthest flights among all boobies, and as mentioned above, high wing loading favors faster speed and shorter foraging times (Brewer and Hertel 2007). On the other hand, Peruvian and Blue-footed Boobies also showed a similar high wing loading, contrary to my prediction for a more coastal species. Although being significantly smaller, higher wing loading allows for faster speeds and therefore the ability to cover greater areas, reduce the prey search time, and return sooner to the colonies. Unlike the three pelagic species that typically produce a single egg, both coastal species typically produce 2-3 egg clutches. They return to their islands on the same day after foraging and may even perform several foraging trips per day during the nesting season (Zavalaga et al. 2007, Zavalaga et al. 2008, Ludynia et al. 2010). Perhaps faster flights, and hence high wing loading, may have allowed for larger clutch sizes in these coastal species.

Red-footed Boobies show a particular departure from the common foraging and nesting strategies in boobies, using aerial pursuit foraging and tree top nesting. This is observed in an intermediate aspect ratio and low wing loading compared to the other pelagic boobies. This is partly a result of a small body mass (low wing loading) but Hertel and Ballance (1999) found their wing loading to be lower than predicted for their body mass. They suggested that the Red-footed Boobies' wing morphology would be reflecting a compromise between low flight cost and high maneuverability required for aerial pursuit.
Pelagic boobies showed significant differences from coastal boobies in their planform shape as predicted, favoring more aft-swept wings that are more efficient for long sustained flight. Relative warp analysis grouped the two coastal boobies on warp 1 (Fig. 10) as having less aft-swept wings and a deeper notch in the proximal wing base compared with the pelagic boobies. Although these pelagic boobies may differ somewhat in their specific foraging strategies, aft-swept wings reduce energy expenditure by increasing lift (Burkett, 1989; van Dam et al., 1991a,b, Lockwood et al. 1998), either for sustained long flights (Masked and Brown Boobies) or highly maneuverable behavior (Red-footed Boobies). Brewer & Hertel (2007) suggested that a pronounced notch close to the wing base might increase lift during take off. A deeper notch in the coastal boobies might increase lift during take off to help compensate for their high wing loading. Relative warp 2 separated only the Brown Booby as having a straighter leading edge, which might be related to their shorter flights from their breeding colonies compared to the other pelagic species; this booby is also the least pelagic of the pelagic species.

Wing and beak morphology and character displacement in coastal Boobies

Both coastal boobies showed overall similar body masses. However, both species throughout their range showed significant reversed sexual dimorphism (RSD), with females being larger than males, as described previously for these (del Hoyo et al. 1992, Zavalaga et al. 2009, Weismerkisch et al. 2009) and other booby species (del Hoyo et al. 1992, Anderson & Ricklefs 1992, Weimerskirch et al. 2006, Weismerskich et al. 2009). Sexual dimorphism in seabirds appears to have important implications during the breeding season where male boobies usually remain longer around the nest than females, tend to make shorter foraging trips, display more territorial behaviors, and sometimes extra pair copulations (Gilardi 1992, Osorio-Beristain & Drummond 1998, Weismerskich et al. 2009). On the other hand, larger body sizes would allow soaring birds to acquire faster flight speeds and therefore perform longer flights (Shaffer et al. 2001, Weimerskirch et al. 2006). Also, differences in body mass in between sexes both Blue-footed and Peruvian Boobies in the allopatric sites (El Rancho, Pajaros, and Mazorca islands) were larger than in the sympatric site.

Most of the data support character displacement given that Peruvian and Blue-footed Boobies showed significant shifts in their beak and wing morphologies in the sympatric site in northern Peru; this suggests a mechanism to minimize potential competition. When combining sexes, Blue-footed Boobies were larger than
Peruvian Boobies only in the sympatric site, suggesting character displacement. This concurs with descriptions by Grant (1972) where body sizes in birds differ in the sites of sympatry and are similar in the allopatric sites.

Beak length was strongly dimorphic in both species at all sites as was body mass, with females having longer beaks than males. When combining sexes, beak length in Peruvian Boobies was significantly smaller at Lobos de Tierra (sympatric site) than other Peruvian Boobies. The same pattern could be observed in relative beak length, where beaks were smaller in Peruvian Boobies in the sympatric site compared to the same or other species at any locality. This indicates potential character displacement in the sympatric site related to prey selection. Although Peruvian Anchovy is the main prey item of most seabirds in the Humboldt Current system, availability may vary from season to season depending on the strength of El Niño events (Chavez et al. 2003, Gutierrez et al. 2007). During moderate or strong El Niño years or when sea surface temperature rises (Kelvin waves, etc.), Peruvian Anchovy, which is highly abundant during normal years, may be less accessible for both species of boobies and stronger competition may arise and ecological segregation in prey type could occur. Beak shape showed an unclear pattern, where beaks of Blue-footed Boobies at the allopatric site (El Rancho) were significantly wider than beaks at other localities (except with Peruvian Boobies in the sympatric site, although they still appeared to be slightly smaller than Blue-footed Boobies). This could indicate that Blue-footed Boobies' wider beak allows them to potentially capture a broader variety of prey as shown by Castillo-Guerrero and Mellink (2010). In the sympatric site (Lobos de Tierra), although Blue-footed Boobies feed mainly on Peruvian Anchovy, they can capture a broader range of prey species compared to Peruvian Boobies, which exclusively consume Peruvian Anchovy (Engraulis ringens) and occasionally Peruvian Silverslide (Odonthestes regia) (pers. obs.). Morphological differences in beak size and shape may become important when harsh conditions arise, such as El Niño or other warming events, and prey is scarce, or when stronger pressures such as breeding or dispersal occur and individuals are subject to more strenuous conditions.

There were significant differences in aspect ratio in the sympatric site between coastal boobies, which partially matched the predictions. Blue-footed boobies had a higher aspect ratio than Peruvian Boobies at all sites, and no shift was detected, so this parameter supported ecological segregation more than character displacement. Higher aspect ratio wings are considered to be more energetically efficient for sustained flight in open habitats such as over the open ocean, where some birds such as albatrosses, which have the highest aspect ratio wings, can take
advantage of strong winds in certain regions as a source of energy for sustained flight (Savile 1957). In the Eastern Tropical Pacific winds are somewhat weak as in most of the tropical region, but even more so when the strong influences of El Niño are common (Fiedler 2002). Nonetheless, Blue-footed Boobies' higher aspect ratio could be reflecting their more pelagic habits and their longer breeding (Castillo-Guerrero & Mellink 2002) and non-breeding dispersal (del Hoyo et al. 1992).

Sexual dimorphism in wing loading occurred only in the allopatric sites, showing a strong correlation with body mass. Wing loading between sexes converged towards the sympatric site, which suggests that boobies are exploiting similar flight speeds and foraging areas, and could be explained by the high abundance of prey in northern Peru. Peruvian Boobies are well known for feeding primarily on Peruvian Anchovy. Similarly, Blue-footed Boobies feed largely on Peruvian Anchovy in the sympatric site (Zavalaga et al. 2008). Lobos de Tierra Island is strongly influenced by the Humboldt Current and the surrounding areas show high degrees of upwelling where Peruvian Anchovy is abundant. Therefore different morphologies related to the optimization of flight and ecological segregation in parameters other than foraging distance may have been selected for in the sympatric site in northern Peru. Zavalaga et al. (2007) also found no differences in foraging areas between males and females of both species in Lobos de Tierra Island, as well as no difference in diving depth, which could be explained by the similar wing loading values.

Although aspect ratio differed significantly between these two species and no shift was detected in the sympatric site, relative warp analysis detected subtle differences in wing planform shape as predicted for character displacement. Relative warp 1 described aft-swept wings in Blue-footed Boobies along all their range. Aft-swept wings are associated with more efficient flight and higher maneuverability (Burkett, 1989; van Dam et al., 1991a,b, Lockwood et al. 1998), which concurs with their ability to control and direct their plunges while foraging. Most coastal boobies showed aft-swept wings, except female Peruvian Boobies at the sympatric site, as opposed to the male Blue-footed Boobies that showed the lowest values for warp 1. This reflects potential character displacement in these two groups, where female Peruvian Boobies are capable of attaining greater lift and therefore flying farther from the island, and male Blue-footed Boobies would be more restricted to foraging closer to the island. Female Peruvian Boobies could be using this mechanism to exploit longer and more efficient flights as discussed above.
Relative warp 2 described greater curvature at the mid wing, which is known to increase wing efficiency, agility, and maneuverability (Burkett, 1989; van Dam et al., 1991). Peruvian Boobies had a greater curvature at the mid wing, which was predicted to be greater for the Blue-footed Booby as a result of its more pelagic habits. This difference might be explained by their different nesting behaviors. Unlike Blue-footed Boobies, Peruvian Boobies commonly nest on cliffs (del Hoyo et al. 1992), which may have selected for better maneuverability to access difficult nesting spots and compensate for strong wind changes due to the proximity to island rock walls.

No significant latitudinal gradient was detected in body mass or wing length for the coastal boobies, but more information may be required for Blue-footed Boobies. There was no evidence in support of Allen's or Bergmann's rule; Blue-footed Boobies even showed an opposite trend to Bergmann's rule with increasing size with decreasing latitude in the sympatric site. The significant differences found in the sympatric site, Lobos de Tierra Island, suggest potential character displacement in foraging and flight parameters. The unique characteristics of northern Peru with high levels of primary productivity and high diversity of prey as a result of mixing water masses from the south (Humboldt Current) and the north (Equatorial Current), and the selective pressures present in a strong upwelling system where environmental variability has strong effects, may have shaped species in this region to cope and allow flexibility to face such conditions and reduce competitive interactions. Zavalaga et al. (2007) in northern Peru, and Castillo-Guerrero and Mellink (2007) in Mexico, found no differences between male and female Blue-footed Boobies in certain foraging patterns, suggesting overlap in foraging strategies. The same pattern was found for Peruvian Boobies in northern Peru (Zavalaga et al. 2010) and northern Chile (Ludynia et al. 2009). However, other parameters did show some segregation, such as dive depths and prey size. Castillo-Guerrero and Mellink (2007) argued that sexual dimorphism in morphological parameters could be manifested when conditions are not favorable. Their research also shows differences in foraging strategies (i.e., foraging distances) between these two species in the sympatric site. Morphological differences as a result of potential character displacement could also be reflected in foraging patterns when conditions are not favorable as during El Niño events or other environment warming events. In general, environmental features differ slightly between Mexico, northern Peru, and Chile, but not as significantly to discard the potential for character displacement. Although resources could be patchy in the northern range of Blue-footed Boobies, Mexico's Pacific coast is influenced by the cold California Current, and this effect could still have an influence on these boobies throughout the region, including the ones sampled in this study in the Sea of Cortes. Feeding and nesting strategies are similar in both species, which would indicate potential
overlap in the site of sympatry. Both species have been recorded to forage close to their nesting islands but also to increase their dispersal ranges associated with unfavorable conditions or during non-breeding seasons.

Character displacement as a mechanism to minimize competition between the sympatric ranges of two allopatric species is generally difficult to evaluate, and observational patterns could shed light on potential situations where it occurs (Greenberg & Olsen 2010). In Peruvian and Blue-footed Boobies in northern Peru, where they are sympatric, competitive interactions are very likely to arise. Morphological differences between these two species appear to be exaggerated in most parameters measured suggesting character displacement (Table 7). These differences could become more important during harsh environmental conditions and potentially during breeding seasons, when competitive interactions would be intensified. Studies in foraging parameters during El Niño events or other harsh conditions might show these differences more clearly. Genetic evidence shows that these two booby species likely evolved from a common ancestor about 1 Mya (Patterson et al. 2011). Blue-footed Boobies are more closely related to the other pelagic species and its morphology suggests more pelagic habits compared to the Peruvian Booby, which is consistent with its foraging ecology my results. The Peruvian Booby on the other hand appears to be more specialized on the upwelling Humboldt Current system. Nevertheless the potential for ecological foraging segregation is present in morphological features in these two species that clearly manifest their evolutionary history of sympatry in northern Peru and the effects of selective pressures in this region.

Although boobies generally share a similar foraging style, comparisons within the group showed slight differences in wing morphology that reflect their particular foraging strategies. In closely related species such as these, it would be common to overlook subtle differences in functional design when analyses are performed on simple morphological features (Simons 2010). However, these shape analyses revealed that more subtle differences in wing morphology correlated well with functional differences.

Wing shape in these boobies shows how diversification in functional design allows highly specialized taxa of seabirds to exploit different environments and foraging strategies along most of the tropical Pacific by means of slight modifications in morphology and behavior. This study helps in our understanding of ecological interactions among Pacific sulids and how selective pressures have shaped the ecomorphology of these seabirds in different ecosystems and the diversification of plunge diving seabirds around the world.
Literature Cited


Figure 3. Body mass of all Pacific boobies (mean +/- SE, n=183). PEBO=Peruvian Booby; BFBO=Blue-footed Booby; BRBO=Brown Booby; RFBO=Red-footed Booby; MABO=Masked Booby. Different letters above error bars denote significant difference by Tukey’s HSD (p<0.05).

Figure 4. Aspect ratio of all Pacific boobies (mean +/- SE, n=183). (For abbreviations and other details refer to Fig. 1)

Figure 5. Wing loading of all Pacific boobies (mean +/- SE, n=183). (For abbreviations and other details refer to Fig. 1)
Figure 6. Vectors representation of relative warp 1 for all boobies at higher (+) and lower values (-)

Figure 7. Relative warp 1 scores for all boobies (means and SE).

Figure 8. Vectors representation of relative warp 2 for all boobies at higher (+) and lower values (-)

Figure 9. Relative warp 2 scores for all boobies (means and SE).

Figure 10. Ordination for all boobies species on relative warps 1 (x-axis) and relative warp 2 (y-axis). (For abbreviations and other details refer to Fig. 1)
Figure 11. Body mass of coastal boobies (mean +/- SE, n=130). PEBO=Peruvian Booby
BFBO=Blue-footed Booby, BRBO=Brown Booby, RFBO=Red-footed Booby, MABO=Masked
Booby, f = female, m = male, SYM = sympatric, ALLO = allopatric. Different letters above error
bars denote significant difference by Tukey's HSD (p<0.05). Blue shaded area represents
sympatric site.

Figure 12. Body mass of coastal boobies combining sexes (mean +/- SE, n=130). (For
abbreviations and other details refer to Fig. 11)

Figure 13. Beak length for coastal boobies (mean +/- SE, n=130). (For abbreviations and other
details refer to Fig. 11)
Figure 14. Beak length in coastal boobies combining sexes (mean ± SE, n=130). (For abbreviations and other details refer to Fig. 11)

Figure 15. Relative Beak length for coastal boobies (mean ± SE, n=130). (For abbreviations and other details refer to Fig. 11)

Figure 16. Relative Beak length in coastal boobies combining sexes (mean ± SE, n=130). (For abbreviations and other details refer to Fig. 11)
Figure 17. Beak shape index for coastal boobies (mean +/- SE, n=130).

Figure 18. Beak shape index in coastal boobies combining sexes (mean +/- SE, n=130).

Figure 19. Aspect ratio of coastal boobies combining sexes (mean +/- SE, n=130).
Figure 20. Wing loading of coastal boobies (mean +/- SE, n=130).

Figure 21. Wing loading of coastal boobies combining sexes (mean +/- SE, n=130).

Figure 22. Vectors representation of relative warp 1 at higher (+) and lower values (-).

Figure 23. Relative warp 1 scores (means and SE).

Figure 24. Vectors representation of relative warp 2 at higher (+) and lower values (-).

Figure 25. Relative warp 2 scores (means and SE).
Figure 26. Vectors representation of relative warp 3 at higher (+) and lower values (-).

Figure 27. Relative warp 3 scores (means and SE).

Figure 28. Vectors representation of relative warp 4 at higher (+) and lower values (-).

Figure 29. Relative warp 4 scores (means and SE).

Figure 30. Ordination separating coastal boobies on relative warps 1 (x-axis) and relative warp 2 (y-axis).
Figure 31. Ordination separating coastal boobies combining sexes on relative warps 1 (x-axis) and relative warp 2 (y-axis).

Figure 32. Relative warp 2 for coastal boobies combining sexes (mean +/- SE, n=130).
### Table 1. Three-way factorial ANOVA results for Body Mass.

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### Table 2. Three-way factorial ANOVA results for Beak length.

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### Table 3. Three-way factorial ANOVA results for Beak relative length.

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### Table 4. Two-way factorial ANOVA results for Beak relative length grouping sexes.

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### Table 5. Three-way factorial ANOVA results for Wing loading.

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</tr>
<tr>
<td>SP*SEX</td>
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<td>43.789</td>
<td>0.895</td>
<td>0.346</td>
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<tr>
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<td>220.612</td>
<td>4.511</td>
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<tr>
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<td>6.772</td>
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<tr>
<td>SEX<em>SP</em>SITE</td>
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<td>24.638</td>
<td>0.504</td>
<td>0.479</td>
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<tr>
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<td>122</td>
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Table 6. Three-way factorial ANOVA results for Relative Warp 4.

<table>
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<tr>
<th>Source</th>
<th>df</th>
<th>Mean-Square</th>
<th>F-ratio</th>
<th>P</th>
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<tbody>
<tr>
<td>SEX</td>
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<td>&lt;0.001</td>
<td>2.930</td>
<td>0.090</td>
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<td>0.004</td>
<td>31.459</td>
<td>0.000</td>
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<tr>
<td>SITE</td>
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<td>0.001</td>
<td>5.462</td>
<td>0.021</td>
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<tr>
<td>SEX*SITE</td>
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<td>&lt;0.001</td>
<td>0.804</td>
<td>0.372</td>
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<tr>
<td>SP*SITE</td>
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<td>0.817</td>
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<tr>
<td>SEX*SP</td>
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<td>0.540</td>
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<tr>
<td>SEX<em>SP</em>SITE</td>
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<td>&lt;0.001</td>
<td>2.632</td>
<td>0.107</td>
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<tr>
<td>Error</td>
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<td>&lt;0.001</td>
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Table 7. Morphological evidence of sexual dimorphism and character displacement in coastal boobies in northern Peru.

<table>
<thead>
<tr>
<th>Morphological Character</th>
<th>Sexual dimorphism</th>
<th>Character displacement</th>
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<tbody>
<tr>
<td>Mass</td>
<td>YES</td>
<td>YES</td>
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<tr>
<td>Beak Length</td>
<td>YES</td>
<td>YES</td>
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<tr>
<td>Beak Relative Length</td>
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<td>YES</td>
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<tr>
<td>Beak Shape (width/depth)</td>
<td>NO</td>
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<tr>
<td>Aspect Ratio</td>
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<tr>
<td>Wing Loading</td>
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<td>NO</td>
</tr>
<tr>
<td>Distal wing (W1)</td>
<td>NO</td>
<td>YES (f BOPE/mBOBF)</td>
</tr>
<tr>
<td>Mid wing (W2)</td>
<td>NO</td>
<td>YES</td>
</tr>
<tr>
<td>Transition Mid to Tip (W3)</td>
<td>NO</td>
<td>YES</td>
</tr>
<tr>
<td>Transition Base to Mid (W4)</td>
<td>NO</td>
<td>NO</td>
</tr>
</tbody>
</table>