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COMPARATIVE ECOMORPHOLOGY OF CORMORANTS (*Phalacrocoracidae*) FROM THREE  
MEDITERRANEAN CLIMATE REGIONS

A thesis submitted in partial fulfillment of the requirements  
For the degree of Master of Science in Biology

By

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## ABSTRACT

### COMPARITIVE ECOMORPHOLOGY OF CORMORANTS (*Phalacrocoracidae*) FROM THREE MEDITERRANEAN CLIMATE REGIONS

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Cormorants (*Phalacrocoracidae*) are seabirds that depend on their hind limbs and beak to pursue and capture their prey underwater, rendering these apparatuses critical for their survival. Although the group is cosmopolitan, cormorant communities of three or more sympatric species are only found in mediterranean climate regions characterized by nutrient rich currents. I used morphological parameters (from museum specimens) related to feeding and locomotion in cormorants from three such regions— California, central Chile, and western S. Africa—to assess convergent functional patterns. Morphological designs were explained by feeding category in 8 of 9 focal species, and a higher resemblance in design pattern was seen between California and S. Africa. Discriminant Function Analysis (DFA) was used to create three feeding categories—generalist (G), pelagic (P), and benthic (B)—based on ecological and dietary information from three Californian feeding types (*Phalacrocorax auritus*, *P. penicillatus*, and, *P. pelagicus*) and three S. African types (*P. carbo lucidus*, *P. capensis*, and *P. coronatus*). All six species were classified to their consensus groups with probabilities  $\geq 85\%$ . Chilean species, *P. olivaceous* and *P. bougainvillii*, were assigned by the DFA to their predicted groups G and P, respectively with probabilities  $\geq 82\%$  and 100%, but *P. gaimardi* was not assigned to its predicted group B, but instead was assigned to P, suggesting a more pelagic feeding ecology. Proportional knee and tarsus lengths, and beak depth were found to be the strongest determinants of feeding category and may be useful tools in predicting feeding ecologies of other hind limb pursuit diving waterbirds.

## Introduction

Natural selection favors phenotypes that optimize feeding efficiency (Karr and James 1975, Miles and Ricklefs 1984), unless constrained by heritage or resource scarcity (Cody 1974). Ecomorphology, the interplay between morphology and ecology, is highly significant in determining an organism's fitness because performance is directly related to survival and reproductive output (Wainwright 1994). An organism's feeding ecology can be explained by its morphology (Miles and Ricklefs 1984, Weins 1991b, Wilson and Smith 2002), and even subtle differences in design have significant effects on an organism's ability to exploit its environment (Goodman and Johnson 2011); therefore, morphology offers a reliable and readily obtainable foundation for exploring ecological divergence and convergence.

The manner in which energy is distributed is important for understanding the effects of selection on consumers, the effects consumers have on each other, and the carrying capacity of their system. Stable coexistence of species with similar diets can be explained by differences in feeding strategy and/or foods consumed, and these differences might be reflected in their morphologies. Huxley (1942) and Lack (1947) were the first to relate partitioning of food items by their sizes with body and beak sizes of consumers. Similarly on Christmas Island, five sympatric species of terns were shown to partition marine prey by the same two parameters (Ashmole 1968). Habitat partitioning was shown in a community of sympatric passerine birds by their tarsus and midtoe lengths (Miles and Ricklefs 1984). Hertel and Ballance (1999) demonstrated partitioning among nine pelagic seabird species on Johnston Atoll by the varying shapes of their wings which they depend on for pursuit and capture of their prey. In foot propelled diving seabirds, it has not yet been demonstrated by which characters species segregate.

Cormorants are good study subjects for exploring community segregation and convergent assemblages for the following reasons. First, all employ foot-propelled underwater pursuit diving to capture prey (Ashmole 1971, Johnsgard 1993). Second, they form communities of three or more species only in mediterranean climate regions (del Hoyo *et al.* 1992, Johnsgard 1993)—California, central Chile, the Cape Province of South Africa, the Mediterranean Basin, and southwestern Australia (Aschmann 1973)—which are characterized by a cold nutrient-rich current. Three of these regions, California, central Chile, and the Cape Province of S. Africa are smaller in geographic range, and show a particularly similar species distribution (two to three species of strictly marine feeders, and one species that feeds in inland and marine habitats) that does not occur in the other regions. Third, they are year-round inhabitants in these regions (del Hoyo *et al.* 1992, Table 1). Fourth, they remain near shore (<20 km

from land) to feed (Ashmole 1971), possibly because of their labored flight (Schreiber and Clapp 1987). Lastly, cormorants are known to feed at different dive depths (summarized by Zavalaga and Paredes 1999), and on a range of prey sizes and types (Johnsgard 1993).

Several studies used dietary analyses to explain the coexistence of cormorant species in California (Ainley *et al.* 1981), central Chile (Crawford *et al.* 2006) and southwestern S. Africa (Rand 1960, Crawford *et al.* 2006). Each of these three regions has a non-endemic opportunistic or generalist species that feeds on freshwater and marine prey (Rand 1960, Palmer 1962, Whitfield and Blaber 1979, Ainley *et al.* 1981, Clapp *et al.* 1982, Wilson and Wilson 1988, Johnsgard 1993, Kalmbach 2001, Randall *et al.* 2002, Barquete *et al.* 2008), an endemic solely marine species for which at least half the prey species are pelagic (schooling) throughout the water column (Matthews 1961, Berry 1967, Crawford and Shelton 1978, Ainley *et al.* 1981, Duffy 1983, Talent 1984, Jahncke and Goya 1997a, 1998b, Adams and Klages 1999, Zavalaga and Paredes 1999), and an endemic solely marine species that feeds on benthic prey in the shallow intertidal zone (Coker 1919, Ainley *et al.* 1981, Williams and Cooper 1983, Nysewander 1986, del Hoyo *et al.* 1992, Johnsgard 1993, Hobson 1997, Zavalaga *et al.* 2002, Frere *et al.* 2002, Gandini *et al.* 2005, Crawford *et al.* 2006). The Cape Province of S. Africa has a fourth species, *P. neglectus*. It feeds strictly in marine habitats on pelagic gobies, benthic fish, and crustaceans (Rand 1960, Williams and Burger 1978, Avery 1983) and does not appear to have a feeding counterpart in central Chile (Crawford *et al.* 2006) or California. A summary of the dietary information is available on Table 2. Although diet plays an important role in niche partitioning, niche space cannot easily be quantified completely by diet because it can vary over short time periods (e.g., season to season, year to year). Morphological change occurs more gradually than behavioral change and is a product of environmental pressure over evolutionary time, therefore it provides a more integrated estimate of an organism's niche (Wiens 1991b).

Cormorants rely on their hind limbs to pursue, and on beaks to capture prey. Therefore, for cormorant species living sympatrically, these apparatuses are expected to reveal functional differences. Currently, it is not well known what morphological characteristics are involved in the feeding specialization of foot-propelled pursuit divers. This study is the first to use a suite of morphological characters to determine those most important for functional segregation in cormorants. My objectives are: (1) to assess which morphological characters are most important in predicting foraging specialization in cormorants, (2) to investigate ecomorphological structure within three mediterranean-climate communities, and (3) to initiate a comparative research framework of foot-propelled pursuit-

diving birds. I predict: (a) three functional types within each mediterranean region will correspond to three feeding categories, and (b) allopatric putative ecological counterparts will more closely resemble one another than sympatric species (Fig. 1). Alternatively, differences in morphological traits may be greatly explained by region, or by their degree of relatedness. However, the phylogeny is not well resolved within the cormorant family (see Siegel-Causey 1988, Kennedy *et al.* 2000, Holland *et al.* 2010). This study assumes that differences in morphological design represent functional differences with respect to feeding ecology. Three communities from geographically isolated regions were used to yield a three-way comparison.



## Materials and Methods

### *Data collection*

Morphological measurements were taken from museum skeletons and study skins. Specimens were tagged as to the sex, age class, and the location found. Specimens were obtained from the Natural History Museum of Los Angeles County, the Louisiana State University Museum of Natural History, the Western Foundation of Vertebrate Zoology, the National Museum of Natural History in Washington DC, the Natural History Museum in Tring, UK, and the National Museum of Natural History in Tel Aviv, Israel.

### *Skeletal variables*

The beak of a bird is most intimately related to feeding, making it the most likely trait to reflect anatomical specializations for handling prey. The length of the beak was taken as a measure of the biomechanical advantage at the tip, which is typically the site of prey capture (Bowmaker 1963). This was measured from the distal end of the craniofacial hinge to the distal tip of the beak (Fig. 2A: a). Total head length was taken from the distal end of the beak to tip of the occipital bone (Fig. 2B: a). Beak depth (Fig. 2B: b) and beak width (Fig. 3A: b) were both measured at the nares.

The hind limbs of cormorants are the primary mechanism of propulsive force when pursuing prey, therefore variation in capture method should be reflected in their legs. The length of the knee (the cnemial crest and patella, Fig. 2C: a) and tibiotarsus (Fig. 2C: b) were measured because they are insertion sites for muscles originating from the thigh, but also as origins for muscles that insert onto the tarsometatarsus (tarsus); these muscles are responsible for the kick stroking action. The width of the arc of the stroke is estimated by the length of the tarsus (Fig. 2D: a) as this rotates on the tibiotarsus, and the spread of the proximal phalanges is determined by the width of the distal tarsus (Fig. 2D: b). In order to transform these absolute hind limb values into proportional lengths, skeletal proxies of body mass were necessary.

Mean body masses were taken from Dunning (2007) and were regressed on mean skeletal characters to identify which characters were the best predictors of body size. Mean body masses were cube-root transformed in order to obtain a linear dimension comparable to character lengths. An ordinary linear regression showed that distal tarsus width (Fig. 2D: b), femur head diameter (Fig. 2E: a), and femur length (Fig. 2E: b) were strong predictors of body mass ( $R^2 \geq 0.90$ ,  $P > 0.001$ ) (Table 3); femur length and head diameter have been found previously to strongly predict body mass in a wide range of avian species (Hertel and Campbell 2007).

In order to minimize differences attributable to body size, knee length, tibiotarsus length, and tarsus lengths were divided by femur head diameter, femur length, and distal tarsus width, respectively; beak length and depth were divided by head length and beak width, respectively. This was done to obtain proportional values more associated with design rather than absolute values associated with body size. Skeletal characters were used in only one index so as to maintain independence.

#### *Study skin variables*

The foot and tarsus move together to produce the propulsive stroke, therefore foot size (surface area) might be predictive of specializations in foraging ecology. Proportional foot size was estimated by measuring digits 1 (hallux) and 4, which are positioned approximately 90° to each other during propulsion, multiplying them together, and dividing the resulting value by the square-rooted mean mass. Digits in highly flexed position were measured in sections.

The elongated tails of cormorants have been suggested to offset buoyancy by controlling the tilting of the body by generating downward directed hydrodynamic lift (Ribak *et al.* 2004) which might be predictive of ecological specialization. Proportional tail length was estimated by measuring the distance from the point of articulation between the tail feathers and pygostyle to the most posterior tip, and dividing by cube-rooted mean body mass. All references to morphological characters henceforth indicate proportional values.

Skeletal and foot measurements were obtained using a Brown & Sharp digital caliper model MK IV in 0.01 mm increments. Tail measurements were taken using a stainless steel ruler in 1.0 mm increments. Variables were  $\log_{10}$ -transformed when warranted to improve normality.

#### *Statistical analysis*

Ordinary least-squares regressions of  $\log_{10}$  (cube-rooted body mass) on  $\log_{10}$  (characters lengths) were used to assess the predictive strengths of skeletal characters for males and females of the ten cormorant species (Table 2). I included an additional species (*P. africanus africanus*) to increase the sample size for a more accurate estimate of character to body mass relationships.

In order to find which variables might be convergent, correlations were calculated between regions—California to Chile, California to S. Africa, and Chile to S. Africa—where the three points for both variables were the same index but for putative counterparts from different regions. These three correlations were transformed, averaged, and back transformed by negative hyperbolic tangents to give the common correlation ( $r_c$ ). Variables with

$r_c > 0.5$  were discussed as matching what would be expected of convergent patterns across the three regions for counterparts predicted to feed similarly.

I assessed intraspecific differences between males and females using two-sample t-tests. No skeletal differences ( $P > 0.05$ ) were found. With respect to skin characters, females were found to have a longer tail in one species, and males had a larger foot in one species. These intraspecific differences were smaller than interspecific differences and males and females for these two species were pooled.

Phenotype is a product of phylogenetic conservatism as well as adaptive change (Losos and Miles 1994, Wainwright 1994). In order to attribute functional similarities to adaptive strategies, significant phylogenetic factors should be accounted for. Two matrix types were created, ecomorphological dissimilarity (Euclidean distances for each variable and for the overall design) and a genetic distance (Kennedy *et al.* 2000; Table 4). The ecomorphological dissimilarity matrix was regressed on the genetic distance matrix, and then the regression was tested for significance with a Mantel test (Mantel 1967, Smouse *et al.* 1986, Legendre *et al.* 1994). Regression of matrices results in a correlation value  $r$  and a test statistic  $t$ . The significance of the  $t$  value was tested against the null distribution produced by random permutation, which was performed by holding one matrix constant and permuting the other 999 times. Variables were standardized prior to creating the morphospace. Genetic information was not available for one of the African species, *P. coronatus*, therefore I substituted information from *P. melanoleucos*; these two species have been consistently grouped in the same subgenus, *Microcarbo* (Van Tets 1976, Dorst and Mougín 1979, Siegel-Causey 1988, Kennedy *et al.* 2000), indicating they are close relatives.

Variables significantly related to phylogeny were adjusted using the variance in the genetic information. Principal Component Analysis (PCA) was used to collapse the genetic matrix to capture the phylogenetic signature in the principal component (PC) values. Phylogeny-related variables were regressed on PC1 and PC2 because they accounted for 84% of the total genetic variance and residuals were used as new relatedness-adjusted index values.

Ecomorphological dissimilarity was tested between sympatric and allopatric species, and between similarly-sized and differently-sized sympatric species using a Mantel's test. These factors were tested to see if there was a higher degree of difference in morphology between sympatric species, or between similarly-sized sympatric species; such patterns are suggestive of competition. In the design matrix, a 0 was placed between species of different regions of the same feeding type, and a 1 was placed between species that were sympatric. Cells of the matrix comparing species that were allopatric and not of the same feeding type were designated as missing data.

Multivariate analyses were used to explore functional designs based on skeletal morphology among species. Principal Component Analysis (PCA) reduces multiple variables that may be correlated into new orthogonal variables called principal components. The variance in each principal component is independent and can be attributed to different factors (body size, phylogeny, selection). Because the effects of body size and phylogeny were already addressed, the PCA results were likely reflective of ecological factors. Variables with greater principal component loadings suggest higher functional diversity. Species' PCA factor scores were plotted in a morphospace to illustrate the distributions of their functional designs. Discriminate Function Analysis (DFA) uses variation among groups specified by the researcher to maximize their differences. The feeding ecologies of the California and S. African communities were studied extensively (Rand 1960, Ainley *et al.* 1981, Wilson and Wilson 1988) and appear to segregate into two marine forms (pelagic, benthic), and one generalist (inland and marine) form. The California species (*P. auritus*, *P. penicillatus*, and *P. pelagicus*), and the S. African species (*P. carbo lucidus*, *P. capensis*, and *P. coronatus*) were used to create generalist (G), pelagic (P), and benthic (B) groups, respectively. Two species, *P. pelagicus* from California and *P. carbo lucidus* from S. Africa, had the smallest sample sizes (ten and six, respectively), therefore identical numbers of individuals were randomly selected from remaining species from these regions to match group sizes. Individuals were permuted to ensure that there was no significant effect of individuals selected on the DFA results. Assignments of Chilean species were made by the DFA. Species from the Mediterranean Basin and southwestern Australia were also analyzed by the DFA so as to predict their feeding category and thereby allow for a broader discussion of mediterranean-climate species.

I used a two-way ANOVA to test for significant differences in skin parameters (foot size and tail length) by feeding category and by region to assess whether a pattern of functional segregation was more prominent within regions than across regions. Skin variables were analyzed separately from skeletal characters as they came from different specimens.

PASSaGE 2 (Pattern Analysis, Spatial Statistics and Geographic Exegesis; Rosenberg and Anderson 2011) was used to create the species morphological dissimilarity matrix and to perform Mantel's tests. SYSTAT 11 (2004) was used for all other analyses.

## Results

### *Differences in body size*

An ANOVA followed by Tukey's HSD multiple comparison test indicated that each region has two species of similar size ( $P \geq 0.05$ , Fig. 4). Because prey size is usually proportional to body size, similar-sized sympatric species are more likely to compete over food than species of differing sizes. Therefore, if competition is playing a role in these regions, a greater functional difference is expected between similarly sized species than between species that differ in size.

### *Phylogenetic effects*

Beak length was found to be the only variable significantly related to phylogeny (Table 5), and therefore, required an adjustment. I used the residuals from a regression of beak length on principal components 1 and 2 as my new adjusted beak length values. The remaining variables were not significantly affected. Euclidean distances in morphospace were not significantly affected by phylogeny prior to the adjustment and became even farther ( $t = 1.18$ ,  $P = 0.126$ ) after the adjustment. Body mass was not significantly related to phylogeny ( $R^2 = 0.077$ ,  $P = 0.056$ ).

### *Common correlations by feeding type*

All variables showed common correlations above 0.5 except tail length. Although significance is not assessed by this method, the pattern indicates convergent trends among similar feeding types across regions (Table 6: bottom) given the number of species involved. Foot size showed the highest common correlation; generalist feeders had higher values than benthic feeders in all three regions. Tarsus length ranked second; pelagic feeders had the highest values in Chile and S. Africa, and benthic feeders had the lowest values in all regions. Tibiotarsus and knee lengths were also highest in pelagic feeders from all regions. Chile's projected benthic feeder *P. gaimardi* also showed comparably high values for tibiotarsus and knee length. All three pelagic feeders had the highest beak lengths. Beak depths were highest in all three generalist feeders. Tail length was correlated the least across regions.

### *Skin analysis*

For foot size there was a significant interaction (two-way ANOVA:  $F_{140,4} = 29.0$ ,  $P < 0.001$ ) between feeding category and region, indicating that it was not consistently explained by either factor. Benthic feeders were similar in all three regions, but generalists and pelagic feeders were only similar between California and S. Africa (Fig. 5: top, right). Looking at foot size by region (Fig. 5: top, left), one would expect all species to differ in foot size within region. This is not the case as species in S. Africa (excluding *P. neglectus* which was not compared) were all

similar, in California generalists were similar to pelagic feeders, and in Chile pelagic and benthic feeders were similar.

For tail length I found a significant interaction (two-way ANOVA:  $F_{140,4} = 108$ ,  $P < 0.001$ ) between feeding category and region, indicating that it was also not consistently explained by either factor. Tail lengths for generalist feeders were similar between California and S. Africa, and for pelagic feeders were similar between California and Chile (Fig. 5: bottom, right). Benthic feeders all differed from each other. Chile was the only region that showed three distinct tail lengths as would be expected in all three regions (Fig. 5: bottom, left). Foot size and tail length results did not follow my hypothesis of convergence in design.

#### *Skeletal analysis*

The PCA had knee length as contributing most to factor 1 and tarsus length as contributing most to factor 2 (Table 7). Only factors 1 and 2 were used to construct the morphospace because they accounted for 97.9% of the total variance. These data indicate that from among all the relativized skeletal characters studied for these ten species, knee and tarsus lengths were functionally most diverse. Based on these, functional design can be split into four categories: (1) longer knees and tarsi, (2) shorter knees and longer tarsi, (3) longer knees and shorter tarsi, (4) and shorter knees and tarsi (Fig. 6).

On the PCA ordination, generalists were separated from pelagic feeders on factor 1. Generalists had shorter knees, whereas pelagic feeders had longer knees. Benthic feeders were not well clustered according to knee length, but they were separated from the other two groups on factor 2. Benthic feeders had shorter tarsi than generalists and pelagic feeders. South Africa's *P. neglectus* had a shorter knee; it most closely resembled the generalists but was in a quadrant of benthic feeders (Fig. 6).

The DFA showed similar results to the PCA, with knee and tarsus lengths most important in discriminating all three feeding groups on axis 1 (Table 9; Fig. 7). Pelagic feeders had the longest knees in all regions and longest tarsi in Chile and S. Africa. Benthic feeders had the shortest tarsi in all three regions. Beak depth was most heavily loaded on axis 2 and was important for discriminating generalist feeders from other groups; beak depths were highest in generalists in all three regions.

Two of Chile's species were assigned to their predicted groups with high certainty (Table 10: top). The first species (*P. olivaceus*) was assigned to the generalist category as predicted with a mean probability of 84.8%. The second species (*P. bougainvillii*) was assigned to the pelagic group as predicted with a mean probability of 100%.

This species had the longest knee of all 10 species and longest tarsus in its region. The last Chilean species (*P. gaimardi*) was not assigned to the predicted benthic group, instead it was assigned to the pelagic group with an 85.7% probability. This unexpected assignment can be attributable to its knee length which is unusually long for a benthic feeder.

Genetic information was not available for most of the non-focal species, therefore a separate DFA was done on these species using non-phylogenetic adjusted data. Consensus groups were created using the same six species from California and S. Africa. One individual of the S. African species *P. carbo lucidus* was misclassified, but this did not alter species assignments (Table 10: bottom). South Africa's *P. neglectus* (species without counterparts) was assigned to the generalist group with 100% probability. The Mediterranean Basin has three species (*P. aristotelis*, *P. pygmaeus*, and *P. carbo sinensis*), and each was assigned to a different category with high probabilities. Southwestern Australia has four species, three of which (*P. sulcirostris*, *P. carbo novaehollandiae*, and *P. varius*) were assigned to the generalists group with probabilities of 66.1%, 97.7%, and 53.3%, respectively. The fourth Australian species (*P. melanoleucos*) was assigned to the benthic group with a 100% probability.

A Mantel test revealed a correlation ( $r = 0.419$ ) between Euclidean distances and a categorization of species comparisons as sympatric or of the same feeding group. Significantly greater dissimilarity was found among sympatric species than among allopatric species within the same feeding category ( $t = 4.57$ ,  $P = 0.003$ , Table 8). A negative correlation ( $r = 0.423$ ) was seen between Euclidean distances and body sizes. Sympatric species of similar body sizes tended to have more similar morphological designs than sympatric species of different body sizes, but this was not significant ( $t = 1.75$ ,  $P = 0.08$ ).

## Discussion

Results of the analyses supported my prediction of three distinct feeding designs in California and S. Africa. Chilean species were assigned to two of three groups, generalist and pelagic. The three Mediterranean Basin species were assigned to all three groups, and Australian species were assigned to two of three groups. Knee and tarsus length appear to be most important in discriminating all three feeding types, whereas beak depth was primarily important for distinguishing generalists from other groups.

### *Beak*

The DFA revealed that beak depth showed high diversity and was important for segregating generalists from other species because they had the deepest beaks in all three regions. Beak depth has been demonstrated to be associated with bite force (Herrel *et al.* 2004), and in generalist cormorants appears to relate to the wide geographic range and high prey diversity. Beak depth was also important in distinguishing benthic feeders from other groups as they tended to have the shallowest beaks.

Beak length was found to be significantly related to phylogeny and was only highly loaded in the non-phylogeny adjusted DFA, suggesting it might be reflective of the ancestral condition. Nonetheless, beak length was found to be highest in all three pelagic feeders, which might indicate that it offers some functional advantage for their specific feeding style. Generally, a longer beak or out-lever emphasizes tip closure speed over closing power (Raikow 1970). Burger (1977) studied four of the S. African cormorants in this sample and found *P. capensis* to have the least proportional jaw muscle mass, supporting my finding that beak closing power is not necessarily emphasized in this feeding category.

### *Leg*

Both multivariate analyses (PCA and adjusted DFA) identified knee length as most diverse of all characters used, suggesting high functional significance in hind limb myology. The cnemial crest and patella (essentially an extension of the cnemial crest) are anterior to the knee joint and provide both an insertion for the quadriceps tendon, and an origin for muscles that flex and extend the tarsus and foot (Owre 1976), actions responsible for propulsion. In many aquatic birds, most notably in foot propelled-divers such as loons, grebes, and cormorants, the knee is long (Shufeldt 1913; personal observation) which is likely an adaptation to an aquatic environment.

Both multivariate analyses (PCA and adjusted DFA) identified tarsus length as highly diverse and strongly predictive of feeding categories, suggesting a high functional significance in stroke width. Hind limb propulsion is



primarily attributable to oscillation of the tarsus, which terminates at the foot, therefore longer tarsi produce wider strokes.

Tibiotarsus length was less diverse than knee or tarsus lengths, suggesting a more limited functional role. An inter-familial comparison of *P. auritus* and *Anhinga anhinga leucogaster* (which employs a more ambush-like strategy; del Hoyo *et al.* 1992) revealed a subtle difference in proportional tibiotarsus (34.2 vs. 35.1) but substantial differences in patellar (4.2 vs. 1.6) and tarsal (20.4 vs. 16.1) lengths supporting my findings.

#### *Foot and tail*

A relationship between foot size or tail length and feeding category showed no consistent pattern across regions. Foot size tended to be higher in generalist than in benthic species and pelagic feeders did not show any consistent ranking pattern across regions. Tail lengths tended to be shorter in pelagic feeders, shorter than generalists in two regions, and shorter than benthic feeders in all regions. This may indicate that pelagic feeders rely less on their tail for pitch control, which was the function associated with the tail in cormorants (Ribak *et al.* 2004) and birds in general (Pennycuick 1975, Tucker 1992). Two cases of dimorphisms were found with respect to the foot and tail. Males of *P. penicillatus* were found to have larger feet than females. The other case involved females of *P. capensis* which had longer tails than males, but this may be a result of my small sample of males (n=3).

#### *Functional types and predictions*

All generalist feeders were characterized by the deepest beaks and substantially shorter knee lengths compared to pelagic species. Deeper beaks are more robust and associated with high bite forces. The generalist species of California, central Chile, and S. Africa are not endemic to mediterranean-climate regions. Their diet is highly variable, but in general these species appear to forage on whatever is in abundance and probably easiest to pursue but maybe not easiest to consume.

Californian and S. African species, *P. auritus* and *P. carbo lucidus*, fit their consensus group (G) with high probabilities. Chile's *P. olivaceous* was also assigned to this group with high probability. Its design appears to facilitate its opportunistic feeding behavior in its wide geographic range. South Africa's *P. neglectus* was also assigned as a generalist with high probability; its diet consists of pelagic gobies, benthic fish, and crustaceans (Rand 1960, Williams and Burger 1978, Avery 1983). One Mediterranean Basin species, *P. carbo sinensis*, was assigned to the generalist group with high probability; it feeds in both freshwater and marine habitats on a wide range of prey with little uniformity in the western Palearctic (Cramp and Simmons 1977). Three of four Australian species were

assigned to the generalist group with varying probabilities. *Phalacrocorax carbo novaehollandiae* was assigned with high probability, whereas *P. sulcirostris* and *P. varius* were assigned with low probabilities. All four Australian species feed in marine and freshwater habitats and have extensive geographic distributions (del Hoyo *et al.* 1992, Johnsgard 1993).

All pelagic feeders were characterized by the longest knees, tibiotarsi, and beaks; in Chile and S. Africa, pelagic species also had the longest tarsi. This design appears to facilitate pursuing and capturing fast-moving pelagic prey. Dietary information on pelagic feeders from Chile and S. Africa, *P. bougainvillii* and *P. capensis*, indicate that these species are specialized for feeding on anchovy and sardine. Dietary studies on California's pelagic feeder, *P. penicillatus*, along the species' entire range demonstrated a more diverse diet consisting of roughly equal numbers of schooling and of solitary fish (Ainley *et al.* 1981, Talent 1984); this appears to be reflected in its shorter tarsus compared to its pelagic counterparts.

Californian and S. African species, *P. penicillatus* and *P. capensis*, fit their consensus group (P) with high probabilities and no misclassifications, indicating that these species follow a convergent design. Chile's *P. bougainvillii* was assigned to this group with high probability. The pelagic design appears to facilitate with the capture of fast-moving schooling fish commonly found in the open water column. One Mediterranean Basin species, *P. aristotelis*, was assigned to this group and its dietary information indicates that it mostly feeds on pelagic fish (Cramp and Simmons 1977). No Australian species was assigned to this category, suggesting that the southwestern Australian coast might not have a pelagic fish specialist.

All benthic feeders were characterized by the shortest tarsi (foot stroke out-lever), which decreases the width of the stroke and generally increases mechanical advantage at the tip (site of the foot). Benthic feeders also tended to have small feet, being smallest in California and S. Africa. A short tarsus and small foot would likely facilitate the capture of prey that is associated with refuges as it emphasizes acceleration rather than speed. Benthic feeders had shorter tibiotarsi, knees, and beaks than pelagic feeders, suggesting they are not designed for capturing fast schooling prey; however, *P. gaimardi* (a putative benthic feeder from Chile) had a knee length comparable to pelagic feeders which might indicate that its feeding ecology differs from its feeding counterparts. Benthic feeders also had shallower beaks than generalists, suggesting they are not designed for a highly variable diet. Dietary information on the three benthic feeders indicates they primarily feed on fish in the shallow (<10 m) intertidal zone. Chile's *P. gaimardi* was also documented to feed heavily on pelagic prey (Murphy 1936, Duffy 1983) such as

anchovy. The ability of *P. gaimardi* to feed on fast moving pelagic prey might be reflected in its longer hind limb characters (excluding the tarsus) compared to its benthic counterparts.

Californian and S. African species, *P. pelagicus* and *P. coronatus*, fit their consensus group (B) with high probabilities. Chile's *P. gaimardi* was not assigned to this group, which was not congruent with my predictions. Instead this species was assigned to the pelagic group with high probability likely because of its longer knee and tibiotarsus. One species from the Mediterranean Basin, *P. pygmaeus*, was assigned to the benthic group with high probability. Freshwater fish appear to make up a large part of its diet in eastern Europe and the adjacent former USSR (Dementiev and Gladkov 1951, Andone *et al.* 1969). Australia's *P. melanoleucos* was assigned to the benthic group with high probability; about half (by mass) of its diet was crustaceans (Serventy and Whittel 1962, Marchant and Higgins 1990).

#### *Competitive interactions*

Euclidean distances were significantly greater among sympatric counterparts of different feeding categories than among allopatric species of the same feeding categories, suggesting that segregation is inflated among species within regions. This might be attributable to competitive interactions or to similar selective pressures in each region.

Euclidean distances did not differ between similarly sized sympatric species than between differently sized sympatric species (Fig. 4). However, species that were of similar sizes always consisted of a generalist form (capable of feeding in freshwater habitats) and a form that was solely marine; two or more strictly marine dwellers were never similarly sized.

Regions with mediterranean environmental conditions appear to select for specialized ecomorphological adaptations in cormorants inhabiting these regions. Cold nutrient-rich upwelling currents characteristic of these zones result in high levels fish biomass (Jennings *et al.* 2001), and these are fed on by a multitude of organisms including seabirds. Cormorant communities of more than two species are only found in these regions (del Hoyo *et al.* 1992, Johnsgard 1993) and appear to segregate by targeting different prey types. This segregation appears to be reflected in their morphological designs, particularly in the hind limb. Although not conclusive, I interpret the functional segregation observed in cormorants in these three mediterranean climates to be suggestive of niche convergence and competitive interactions.

### Literature Cited

- Adams, N. J., Klages, N. T. W. 1999. Foraging effort and prey choice in Cape gannets. *South African Journal of Marine Science* 21: 157-163.
- Ainley, D. G., Anderson D. W., and Kelly, P. R. 1981. Feeding ecology of marine cormorants in southwestern North America. *Condor* 83: 120-131.
- Ainley, D. G., and Boekelheide, R. J. 1990. *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford University Press, Stanford, California.
- Andone, G., Almasan, H., Rudu, D., Andone, L., Chirac, E., and Sclarletescu, G. 1969. Cercetare asupra pasarilor ichiof, age din delta Dunarii. *Inst. cercet. Pisc. Studi si Cercetari (Romania)* 27: 133-183.
- Aschmann, H. 1973. Distribution and peculiarity of Mediterranean ecosystems. In F. di Castri and H. A. Mooney (Eds). *Mediterranean Type Ecosystems*. Springer-Verlag, New-York, New York. pp. 11-20.
- Ashmole, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns. *Systematic Zoology* 17: 292-304.
- Ashmole, N. P. 1971. Seabird ecology and the marine environment. In Farner, D.S., King J. R., and Parkes, K. C. (Eds). *Avian Biology*. Volume 1. Academic Press, New York, New York. pp. 223-286.
- Avery, G. 1983. Bank cormorants *Phalacrocorax neglectus* taking Cape rock lobster *Jasus lalandii*. *Cormorant* 11: 45-48.
- Barquete, V., Bugoni, L., and Vooren, C. M. 2008. Diet of Neotropical cormorant (*Phalacrocorax brasilianus*) in an estuarine environment. *Marine Biology* 153: 431-443.
- Berry, H. H. 1976. Physiological and behavioral ecology of the Cape cormorant *Phalacrocorax capensis*. *Madoqua*, 9: 57-62.
- Bowmaker, A. P. 1963. Cormorant predation on two central African lakes. *Ostrich* 34: 2-26.
- Burger, A. E. 1977. Functional anatomy of feeding apparatus of four South African cormorants. *Zoologica Africana* 13: 81-102.
- Clapp, R. B., Banks, R. C., Morgan-Jacobs, D., and Hoffman, W. A. 1982. *Marine Birds of Southeastern United States and Gulf of Mexico*. Part. 1. Gaviiformes through Pelecaniformes. U.S. Fish & Wildl. Serv., Off. Biol. Serv. Washington, D.C. FSW/OBS 82/01.
- Cody, M. L. 1974. Optimization in ecology. *Science* 183: 1156-1164.

- Coker, R. C. 1919. Habits and economic relations of the guano birds of Peru. *Proceedings of the United States National Museum* 56: 449-511.
- Cramp, S., and Simmons, K. E. L. 1977. *The Birds of the Western Palearctic*. Vol. 1. Oxford University Press, Oxford, UK.
- Crawford, R. J. M., Goya, E., Roux, J-P., and Zavalaga, C. B. 2006. Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems. *African Journal of Marine Science* 28: 553-560.
- Crawford, R. J. M., and Shelton, P. A. 1978. Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. *Biological Conservation* 14: 85-109.
- del Hoyo, J., Elliot, A., and Sargatal, J. 1992. *Handbook of the Birds of the World*. Vol. 1. Lynx Edicions, Barcelona.
- Dementiev, G. P., and Gladkov, N. A. 1951. Birds of the Soviet Union. Vol. 1. Sovetskaya Nauka, Moscow. (In Russian. Translated in 1966 by the Israel Program for Scientific Translations, Jerusalem.)
- Dorst, J., and Mougín, J. L. 1979. Order Pelecaniformes. In Mayr, E., and Cottrell, G. W. (Eds). *Check List of Birds of the World*. Vol. 1. 2<sup>nd</sup> edition. Museum of Comparative Zoology, Cambridge, Massachusetts.
- Duffy, D. C. 1983. The foraging ecology of Peruvian seabirds. *Auk* 100: 800-810.
- Dunning, J. B. Jr. 2007. *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton, Florida.
- Frere, E., Quintana, F., and Gandini, P. 2002. Diving behavior of the Red-Legged cormorant in southeastern Patagonia, Argentina. *Condor* 104: 440-444.
- Gandini, P., Frere, E., and Quintana, F. 2005. Feeding performance and foraging area of the Red-Legged cormorant. *Waterbirds* 28: 41-45.
- Goodman, B. A., and Johnson, P. T. J. 2011. Ecomorphology and disease: cryptic effects of parasitism on host habitat use, thermoregulation, and predator avoidance. *Ecology* 92: 542-548.
- Herrel, A., Podos, J., Huber, S. K., and Hendry, A. P. 2004. Evolution of bite force in Darwin's finches: a key role for head width. *Journal of Evolutionary Biology* 18: 669-675.
- Hertel, F., and Campbell Jr., K. E. 2007. The antitrochanter of birds: form and function in balance. *Auk*, 124: 789-805.
- Hertel, F., and Ballance, L. T. 1999. Wing ecomorphology of seabirds from Johnston Atoll. *Condor* 101: 549-556.

- Hobson, K. A. 1997. Pelagic Cormorant *Phalacrocorax Pelagicus*. In Pool, A., and Gill, F. (Eds). *The Birds of North America*. No. 73. American Ornithologists' Union, Academy of Natural Sciences of Philadelphia, Washington, D.C.
- Holland, B. R., Hamish, S. G., Worthy, T. H., and Kennedy, M. 2010. Identifying cliques of convergent characters: concerted evolution in the cormorants and shags. *Systematic Biology* 59: 433-445.
- Huxley, J. 1942. *Evolution: The modern synthesis*. Allen and Unwin Press, London, UK.
- Jahncke, J., and Goya, E. 1997. Variacion latitudinal y estacional en la dieta del guanay (*Leucocarbo bougainvillii*) y el piquero peruano (*Sula variegata*) en la costa Peruana. *Boletín del Instituto del Mar del Perú* 16: 23-41.
- Jennings, S. M. 2001. *Marine fisheries ecology*. Blackwell Science Ltd., Oxford, UK.
- Johnsgard, P. A. 1993. *Cormorants, darters, and pelicans of the world*. Smithsonian Institutional Press, Washington, D.C.
- Kalmbach, E., Ramsay, S. C., Helmut, W., and Becker, P. H. 2001. A study of neotropical cormorants in central Chile: possible effects of El Niño. *Waterbirds* 24: 345-351.
- Karr, J. R., and James, F. C. 1975. Ecomorphological configurations and convergent evolution in species and communities. In Cody, M. L., and Diamond, J. M. (Eds). *Ecology and Evolution of Communities*. Cambridge: Belknap Press. pp. 258-291.
- Kennedy, M., Gray, R. D., and Hamish, S. G. 2000. The phylogenetic relationships of the shags and cormorants: can sequence data resolve a disagreement between behavior and morphology? *Molecular Phylogenetics and Evolution* 17: 345-359.
- Lack, D. 1947. *Darwin's finches: an essay on the general biological theory of evolution*. Cambridge University Press, Cambridge, UK.
- Legendre, P., Lapointe, F.-J., and Casgrain, P. 1994. Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48: 1487-1499.
- Losos, J. B., and Miles, D. B. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In Wainwright, P. C., and Reilly, S. M. (Eds). *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago, Illinois. pp. 60-98.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.

- Marchant, S., and Higgins, P. J. 1990. *Handbook of Australian, New Zealand, & Antarctic Birds*. Vol. 1. Oxford University Press, Melbourne, Australia.
- Matthews, J. P. 1961. The pilchard of South West Africa *Sardinops ocellata* and the maasbanker *Trachurus trachurus*. *Bird Predators*. 1957-1958. Investigational Report of the Marine Research Laboratory, South West Africa 3: 1-35.
- Miles, D. B., and Ricklefs, R. E. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* 65: 1629-1640.
- Murphy, R. C. 1936. *Oceanic birds of South America*. American Museum of Natural History. Macmillan Company, New York, New York.
- Nysewander, D. N. 1986. Cormorants (*Phalacrocorax* spp.). In Baird, P. A., and Gould, P. J. (Eds.). *The Breeding Biology and Feeding Ecology of Marine Birds in the Gulf of Alaska*. Environmental Assessment of the Alaskan Continental Shelf, Final Reports, NOAA, Anchorage 45: 207-236.
- Orians, G. H., and Paine, R. T. 1983. Convergent evolution at the community level. In Futuyma, D. J., and Slatkin, M. (Eds). *Coevolution*. Sunderland: Sinauer Associates, Inc. pp. 431-458.
- Owre, O. T. 1967. Adaptations for locomotion and feeding in the anhinga and the Double-Crested cormorant. *Ornithological Monographs* 6: 1-138.
- Palmer, R. S. 1962. *Handbook of North American birds*. Yale University Press, New Haven, Connecticut.
- Pennycuik, C. J. 1975. Mechanics of flight. In D. S. Farner and King J. R. (Eds). *Avian Biology*. Vol. V. pp. 1-75. Academic Press, New York, New York.
- Quintana, F., Yorio, P., Lisnizer, N., Gatto, A., and Soria, G. 2004. Diving behavior and foraging areas of the Neotropic cormorant at a marine colony in Patagonia, Argentina. *The Wilson Bulletin* 116: 83-88.
- Raikow, R. J. 1970. Evolution of diving adaptation in the stiff-tail ducks. *University of California Publications in Zoology* 94: 1-52.
- Rand, R.W., 1960. The distribution, abundance and feeding habits of the cormorants *Phalacrocoracidae* off the south-western coast of the Cape Province. In *The biology of guano-producing seabirds*. Investigational Report of the Sea Fisheries Research Institute, South Africa 42: 1-32.
- Randall, R. M., Tregoning, C., Randall, B. M., and Martin A. P. 2002. Adaptability of great cormorants *Phalacrocorax carbo* in a coastal environment demonstrated by their exploitation of introduced prey

- species and use of artificial breeding sites. *South African Journal of Marine Science* 24: 317-321.
- Ribak, G., Weihs, D., and Arad, Z. 2004. How do cormorants counter buoyancy during submerged swimming? *The Journal of Experimental Biology* 207: 2101-2114.
- Ricklefs, R. E., Travis, J. 1980. A morphological approach to the study of avian community organization. *Auk* 97: 321-338.
- Rosenberg, M. S., and Anderson, C. D. 2011. PASSaGE: Pattern Analysis, Spatial Statistics, and Geographic Exegesis. Version 2. *Methods in Ecology and Evolution* 2: 229-232.
- Schluter, D. 1986. Tests for similarity and convergence of finch communities. *Ecology* 67: 1073-1085.
- Smouse, P. E., Long, J. C., and Sokal, R. R. 1986. Multiple regression and correlation extension of the Mantel test of matrix correspondence. *Systematic Zoology* 35: 627-632.
- Tucker, V. A. 1992. Pitching Equilibrium, Wing span and tail span in a gliding Harris' Hawk, *Parabuteo unicinctus*. *Journal of Experimental Biology* 165: 21-41.
- Van Tets, G. F. 1976. Australasia and the origin of shags and cormorants, *Phalacrocoracidae*. In *Proceedings of the 16th International Ornithological Congress, Canberra, Australia (1974)*. pp. 121-124.
- Schreiber, R. W., and Clapp, R. B. 1987. Pelecaniform feeding ecology. In J. P. Croxall (ed). *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge, UK. pp. 173-188.
- Shufeldt, R. W. 1913. On the patella in the *Phalacrocoracidae*. *Proceedings of the Zoological Society of London* 83: 393-402.
- Siegel-Causey, D. 1988. Phylogeny of *Phalacrocoracidae*. *Condor* 90: 885-905.
- Smith, B. and Wilson, J. B. 2002. Community convergence: ecological and evolutionary. *Folia Geobotanica* 37: 171-183.
- Talent, L. G. 1984. Food habits of the wintering Brandt's cormorant. *The Wilson Bulletin* 96: 130-134.
- Wainwright, P. C., and Reilly, S. M. 1994. *Ecological Morphology: Integrative Organismal Biology*. The University of Chicago Press, Chicago, Illinois.
- Whitfield, A. K. and Blaber, J. M. 1979. Feeding ecology of piscivorous birds at Lake St. Lucia. *Ostrich* 50: 10-20.
- Wiens, J. A. 1991. Ecomorphological comparisons of the shrub-desert avifaunas of Australia and North America. *Oikos* 60: 55-63.

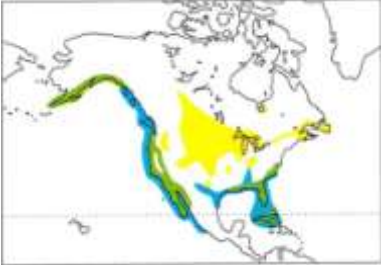





- Williams, A. J., and Burger, A. E. 1978. The ecology of the prey of Cape and Bank cormorants. *Cormorant* 4: 28-29.
- Williams, A. J., and J. Cooper. 1983. The Crowned cormorant: breeding biology, diet and offspring-reduction strategy. *Ostrich* 54: 213-219.
- Wilson, R. P., and Wilson, M. P. T. 1988. Foraging behavior in four sympatric cormorants. *Journal of Animal Ecology* 57: 943-955.
- Zavalaga, C. B. and Paredes, R. 1999. Behavior and diet of the guanay cormorant. *South African Journal of Marine Science* 21: 251-258.

## Appendix A: Tables

**Table 1.**

Habitat and geographic distributions for ten cormorant species (and subspecies if any). Each map represents the distribution of a species including all its subspecies. Yellow and blue colors indicate breeding and non-breeding grounds, respectively. Green color corresponds to year-round occupation (after del Hoyo *et al.* 1992).

Common name <i>Scientific name</i> ( <i>subspecies</i> )	Geographic distribution	
Double-crested Cormorant <i>Phalacrocorax auritus</i> ( <i>albociliatus</i> )	Vancouver Island to the Gulf of California year-round; occurs in marine and inland water.	
Brandt's Cormorant <i>Phalacrocorax penicillatus</i>	Southeast Alaska to Baja California year-round; strictly marine.	
Pelagic Cormorant <i>Phalacrocorax pelagicus</i> ( <i>resplendens</i> )	British Columbia to N.W. Mexico year-round; strictly marine.	
Neotropic Cormorant <i>Phalacrocorax olivaceus</i> ( <i>olivaceus</i> )	Panama to Cape Horn, Chile year-round; occurs in marine and inland waters.	

Guanay Cormorant  
*Phalacrocorax bougainvillii*

Peru to central Chile year-round;  
strictly marine.



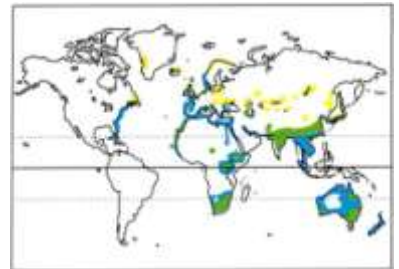
Red-legged Cormorant  
*Phalacrocorax gaimardi*

Peru to south central Chile and  
along the Atlantic coast in S.  
Argentina year-round;  
strictly marine.



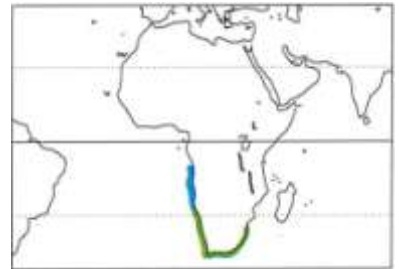
White-breasted Cormorant  
*Phalacrocorax carbo*  
(*lucidus*)

Marine in N.W. Africa, marine  
and inland in S. Africa, and  
inland in E. Africa, year- round.



Cape Cormorant  
*Phalacrocorax capensis*

Namibia and South Africa year-  
-round; almost exclusively  
marine.



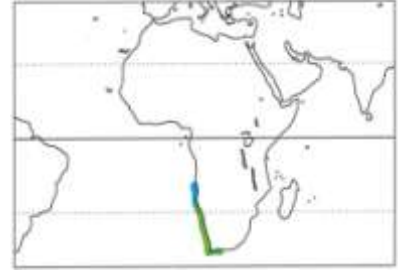
Crowned Cormorant  
*Phalacrocorax africanus*  
(*coronatus*)

Namibia to the southernmost  
tip of Africa; markedly marine.



Bank Cormorant  
*Phalacrocorax neglectus*

Namibia to W. South Africa  
year-round; strictly marine.



**Table 2.**

Feeding categories and hypothesized counterparts based on dietary information. Symbol colors represent regions (black = California, grey = central Chile, and white = Cape Province, S. Africa) and symbol shapes represent feeding categories (square = generalist, triangle = pelagic marine, and circle = benthic). No ecological equivalents exist for S. Africa's *P. neglectus*; it is symbolized by a rhomboid. Symbols are used throughout all subsequent figures.

<b>Feeding category</b>	<b>California</b>	<b>Central Chile</b>	<b>Cape Province</b>
Generalist diet (G); freshwater and marine	<i>P. auritus</i> (■)	<i>P. olivaceous</i> (■)	<i>P. carbo lucidus</i> (□)
Pelagic fish (P); marine only	<i>P. penicillatus</i> (▲)	<i>P. bougainvillii</i> (▲)	<i>P. capensis</i> (Δ)
Benthic prey (B); marine only	<i>P. pelagicus</i> (●)	<i>P. gaimardi</i> (●)	<i>P. coronatus</i> (○)
Pelagic goby, benthic fish & crustaceans; marine only	No equivalent	No equivalent	<i>P. neglectus</i> (◇)

**Table 3.**

Coefficients of determination and *P*-values of  $\log_{10}$  (body mass) regressed on  $\log_{10}$  (characters). A total of 22 means (males and females of 11 species) was used per character.

<b>Skeletal characters</b>	<b>R<sup>2</sup></b>	<b><i>P</i></b>
Distal tarsus width	0.95	<0.001
Femur length	0.94	<0.001
Femur head diameter	0.92	<0.001
Head length	0.85	<0.001
Tibiotarsus length	0.85	<0.001
Tarsus length	0.83	<0.001
Head width	0.80	<0.001
Beak length	0.79	<0.001
Beak width	0.74	<0.001
Knee length	0.50	<0.001
Beak depth	0.31	=0.004

**Table 4.**

Tamura-Nei distance matrix of focal species showing percentage of sequence divergence between species (from Kennedy *et al.* 2000). Letter G, P, and B represent the three feeding categories from table 2. Abbreviations CA, Ch, and Af represent California, Chile, and S. Africa, respectively.

	G <sub>CA</sub>	P <sub>CA</sub>	B <sub>CA</sub>	G <sub>Ch</sub>	P <sub>Ch</sub>	B <sub>Ch</sub>	G <sub>Af</sub>	P <sub>Af</sub>
P <sub>CA</sub>	7.7							
B <sub>CA</sub>	7.8	5.2						
G <sub>Ch</sub>	2.2	7.4	7.4					
P <sub>Ch</sub>	6.0	7.8	7.8	5.7				
B <sub>Ch</sub>	9.0	9.2	10.3	8.5	9.1			
G <sub>Af</sub>	6.7	6.5	6.8	6.4	6.9	9.8		
P <sub>Af</sub>	7.3	6.6	7.1	6.7	7.2	9.5	4.6	
B <sub>Af</sub>	12.2	10.9	11.3	12.0	11.1	10.7	10.6	11.0

**Table 5.**

Mantel test results of ecomorphological dissimilarity and genetic distances. Values in bold indicate significant relationships. Asterisks indicate variables that were  $\log_{10}$  transformed to improve normality.

<b>Index</b>	<b><i>r</i></b>	<b><i>P</i></b>
Beak length*	0.546	<b>0.046</b>
Tibiotarsus length	0.313	0.090
Knee length	0.203	0.108
Tail length	0.086	0.324
Tarsus length*	0.035	0.426
Beak depth	-0.106	0.572
Foot size	-0.232	0.790
Morphospace distances	0.371	0.051



**Table 6.** Top: raw skeletal character values for the three feeding categories (G, P, and B; see Table 2) found in California, Chile, and S. Africa. Middle: same but of skin characters. Bottom: common correlation ( $r_c$ ) represents average correlation within same feeding category among regions. Higher common correlation values indicate more convergent design among similar feeding categories; those above 0.5 are marked in bold;  $n$  indicates the sample size. *Phalacrocorax neglectus* (N) was not included in calculating correlations because it had no counterpart in California or Chile.

Skeletal character	California			Chile			S. Africa				
	G	P	B	G	P	B	G	P	B	N	
Tarsus length	65.7	63.8	50.2	53.4	68.0	50.3	61.5	57.2	42.1	60.8	
Beak length	66.1	74.2	52.6	58.9	75.3	60.9	70.3	68.9	37.1	67.1	
Beak depth	14.6	14.3	8.17	14.1	12.7	10.4	16.6	11.1	8.99	12.8	
Tibiotarsus length	107	116	89.7	85.2	120	100	102	95.0	68.1	101	
Knee length	21.0	26.7	20.2	16.1	27.0	23.8	19.4	19.9	12.6	20.0	
$n$	18	36	11	10	10	7	6	21	8	8	
<b>Skin characters</b>											
Digit 4 length	96.4	106	90.9	89.1	96.5	92.4	96.7	81.8	66.6	96.8	
Digit 1 (hallux) length	38.7	36.8	33.9	37.6	32.4	26.8	39.5	31.6	29.8	34.8	
$n$	16	31	13	30	12	12	16	7	9	10	
<b>Index</b>											
Foot size	79.4	83.1	72.5	96.5	63.5	67.2	74.0	74.7	72.3	75.2	<b>0.84</b>
Tarsus length	4.28	4.06	3.71	4.15	4.52	3.88	4.02	4.61	3.84	4.00	<b>0.80</b>
Beak length	0.52	0.55	0.50	0.52	0.57	0.53	0.54	0.55	0.46	0.53	<b>0.75</b>
Beak depth	1.25	1.09	0.88	1.27	1.03	1.01	1.19	1.04	1.14	1.14	<b>0.67</b>
Tibiotarsus length	1.80	1.94	1.72	1.69	2.09	2.01	1.81	1.96	1.56	1.76	<b>0.67</b>
Knee length	2.90	3.67	3.26	2.69	3.93	3.91	2.82	3.42	2.53	2.82	<b>0.63</b>
Tail length	13.9	12.2	14.6	19.2	11.1	12.8	13.5	13.7	18.4	12.5	0.31

**Table 7.**

Principal Component Analysis factors 1 and 2, and the percent variance explained by each. Highly loaded variables are represented in bold.

<b>Index</b>	<b>Factor 1</b>	<b>Factor 2</b>
Knee length	<b>0.510</b>	-0.064
Tarsus length	0.119	<b>0.265</b>
Tibiotarsus	0.156	0.034
Beak depth	-0.070	0.063
Beak length	0.020	0.012
Percent variance explained	77.6	20.3

**Table 8.**

Matrix showing Euclidean distances among species in morphospace. Smaller distances indicate closer resemblance in ecomorphological design. Letter G, P, and B represent the three feeding categories from table 2. Abbreviations CA, Ch, and Af represent California, Chile, and S. Africa, respectively. South Africa's fourth species, *P. neglectus*, is indicated by N.

	G <sub>CA</sub>	P <sub>CA</sub>	B <sub>CA</sub>	G <sub>Ch</sub>	P <sub>Ch</sub>	B <sub>Ch</sub>	G <sub>Af</sub>	P <sub>Af</sub>	B <sub>Af</sub>
P <sub>CA</sub>	2.60								
B <sub>CA</sub>	3.82	3.15							
G <sub>Ch</sub>	0.90	-	-						
P <sub>Ch</sub>	-	2.02	-	4.49					
B <sub>Ch</sub>	-	-	2.74	3.90	2.65				
G <sub>Af</sub>	1.40	-	-	1.44	-	-			
P <sub>Af</sub>	-	1.98	-	-	1.51	-	2.76		
B <sub>Af</sub>	-	-	3.08	-	-	4.54	3.29	4.94	
N <sub>Af</sub>	-	-	-	-	-	-	0.68	2.88	2.73

**Table 9.**

Canonical discriminant functions based on California's and S. Africa's species, and percent variance explained by each for phylogeny-adjusted and original data. Values in bold indicate highly loaded variables.

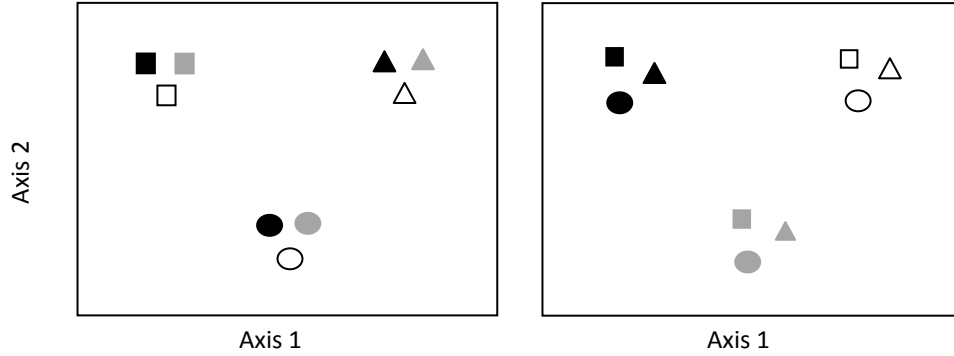
Index	Adjusted		Original	
	Axis 1	Axis 2	Axis 1	Axis 2
Knee length	<b>0.984</b>	-0.244	0.793	<b>-0.604</b>
Tarsus length	<b>0.888</b>	-0.582	0.688	-0.202
Beak depth	0.846	<b>1.189</b>	<b>1.362</b>	0.478
Beak length	0.696	-0.779	0.914	<b>0.769</b>
Tibiotarsus length	0.569	0.702	0.375	-0.429
Percent variance explained	92.4%	7.6%	90.1%	9.9%

**Table 10.**

Top: DFA assignments of individuals of each species. The number of individuals of each species assigned is represented in the column n. Columns G, P, and B represent the three consensus groups formed by species in shaded region; values in each column indicate the number of individuals assigned, and the mean probability with which the assignment was made. The last column shows the overall group assignment and its probability. Bottom: same as top but using non-phylogeny adjusted data.

<b>Species</b>	<b>n</b>	<b>G</b>	<b>P</b>	<b>B</b>	<b>Assignment</b>
<i>P. auritus</i> (CA)	6	6, 100%			G, 100%
<i>P. penicillatus</i> (CA)	6		6, 100%		P, 100%
<i>P. pelagicus</i> (CA)	6			6, 100%	B, 100%
<i>P. carbo lucidus</i> (Af)	6	5, 99.7%		1, 89.9%	G, 84.8%
<i>P. capensis</i> (Af)	6		6, 100%		P, 100%
<i>P. coronatus</i> (Af)	6			6, 100%	B, 100%
<i>P. olivaceus</i> (Ch)	10	9, 91.5%		1, 100%	G, 82.4%
<i>P. bougainvillii</i> (Ch)	10		10, 100%		P, 100%
<i>P. gaimardi</i> (Ch)	7	1, 56.3%	6, 100%		P, 85.7%
<b>Species</b>	<b>n</b>	<b>G</b>	<b>P</b>	<b>B</b>	<b>Assignment</b>
<i>P. auritus</i> (CA)	6	6, 92.0%			G, 92.0%
<i>P. penicillatus</i> (CA)	6		6, 93.3%		P, 93.3%
<i>P. pelagicus</i> (CA)	6			6, 100%	B, 100%
<i>P. carbo lucidus</i> (Af)	6	6, 96.3%			G, 96.3%
<i>P. capensis</i> (Af)	6		6, 99.6%		P, 99.6%
<i>P. coronatus</i> (Af)	6			6, 100%	B, 100%
<i>P. neglectus</i> (Af)	8	8, 100%			G, 100%
<i>P. aristotelis</i> (MB)	5		5, 100%		P, 100%
<i>P. pygmaeus</i> (MB)	1			1, 100%	B, 100%
<i>P. carbo sinensis</i> (MB)	3	3, 99.7%			G, 99.7%
<i>P. sulcirostris</i> (Au)	3	2, 99.1%		1, 100%	G, 66.1%
<i>P. carbo novaehollandiae</i> (Au)	2	2, 97.7%			G, 97.7%
<i>P. varius</i> (Au)	2	1, 98.2%	1, 91.7%		G, 53.3%
<i>P. melanoleucos</i> (Au)	3			3, 100%	B, 100%

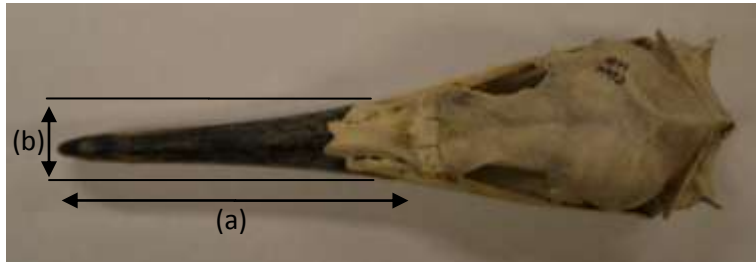
## Appendix B: Figures



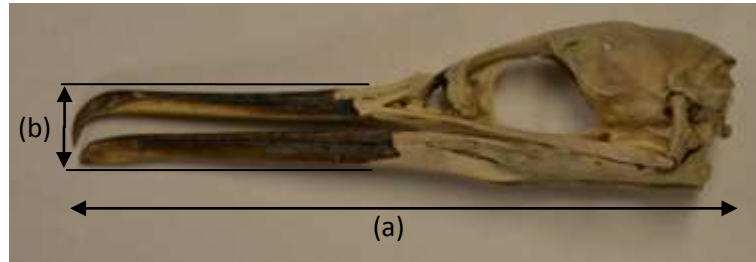
**Fig. 1.**

Diagram of 2-dimensional hypothetical morphospace. Points indicate species, colors indicate regions, and shapes indicate functional types. Axes represent components of variation among morphological variables across species. Left: hypothesized distribution of species by similar functional type. Right: alternative hypothesized species distribution by geography.

A. skull (dorsal view)



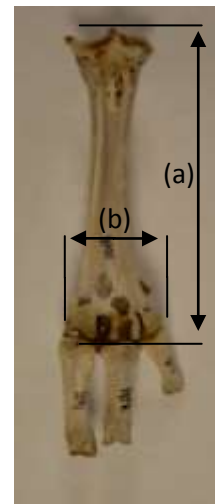
B. skull (lateral view)



C. tibiotarsus (medial view)



D. tarsus (anterior view)



E. femur (anterior view)

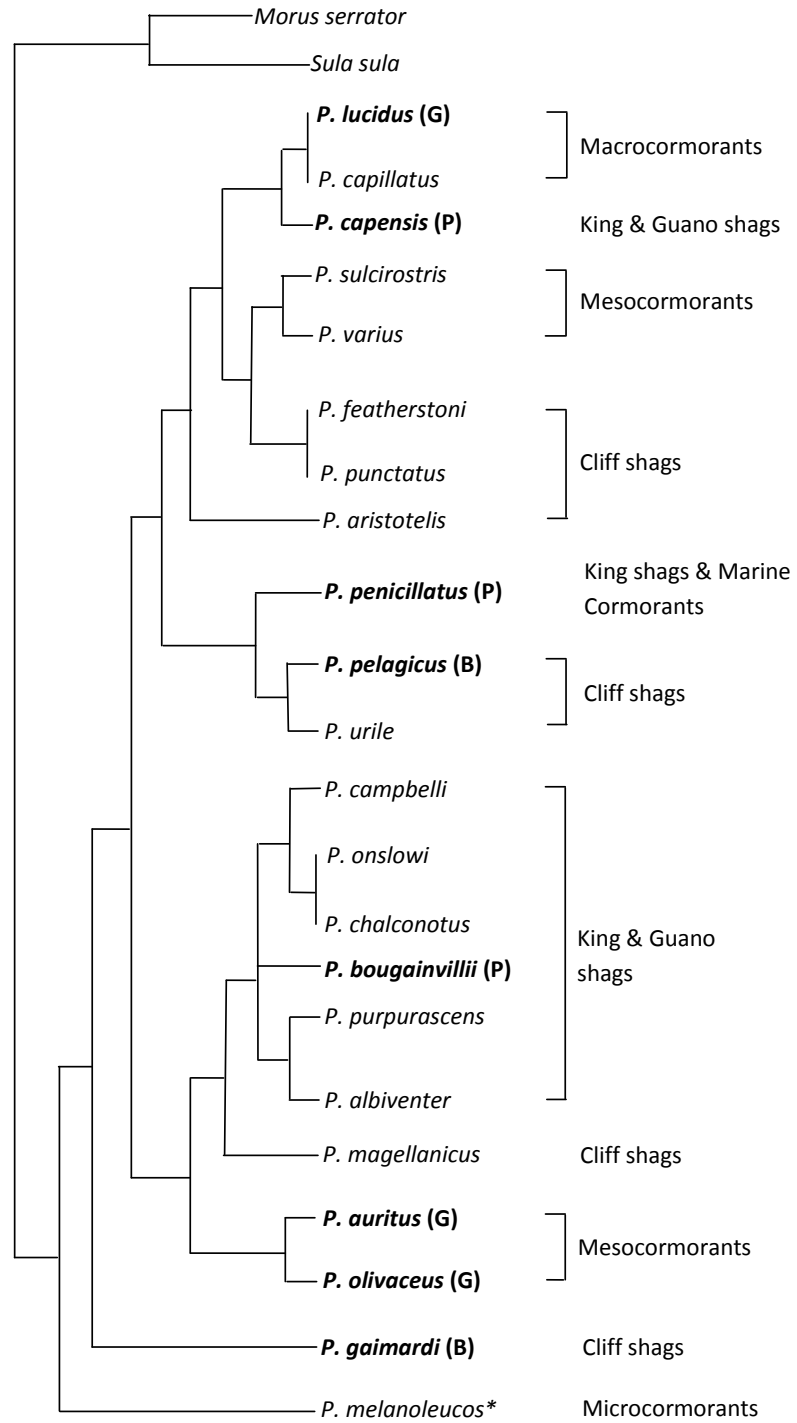


Fig. 2

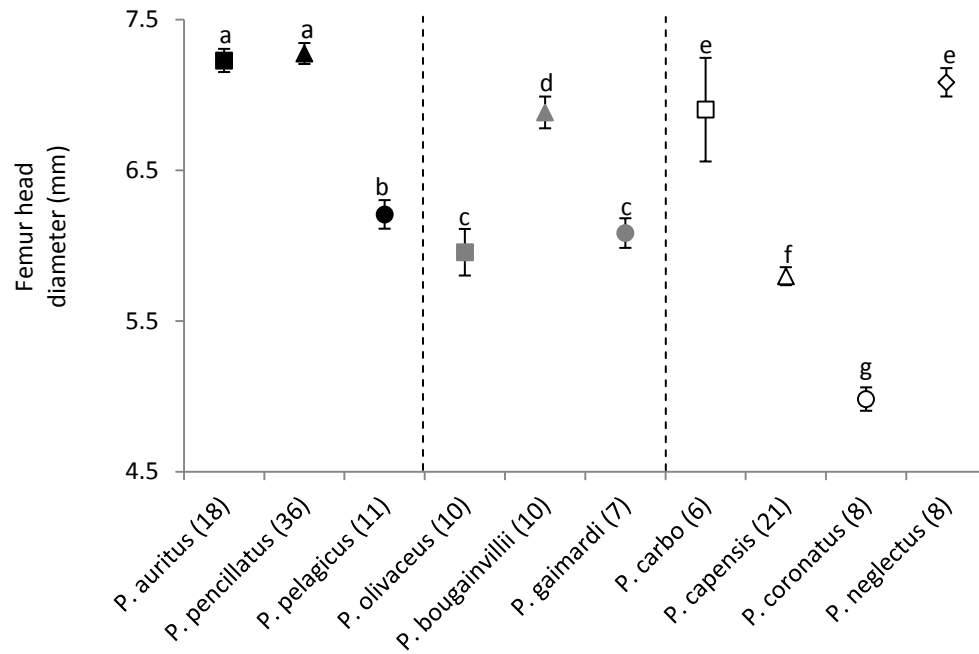
Photographs illustrating morphological measurements taken from skeletons. A: (a) beak width, (b) beak length; B: (a) head length, (b) beak depth; C: (a) knee (cnemial crest + patella) length; (b) tibiotarsus length; D: (a) tarsometatarsus (tarsus) length, (b) distal tarsus width; E: (a) femur head diameter, (b) femur length.

**Fig. 3.**

Maximum likelihood phylogeny generated from sequence data by Kennedy *et al.* (2000). On the right, classification based on Siegel-Causey's (1988) osteological study. Taxa in bold represent species measured in my study. The taxon with an asterisk indicates a species whose phylogenetic information was substituted for a missing focal species.

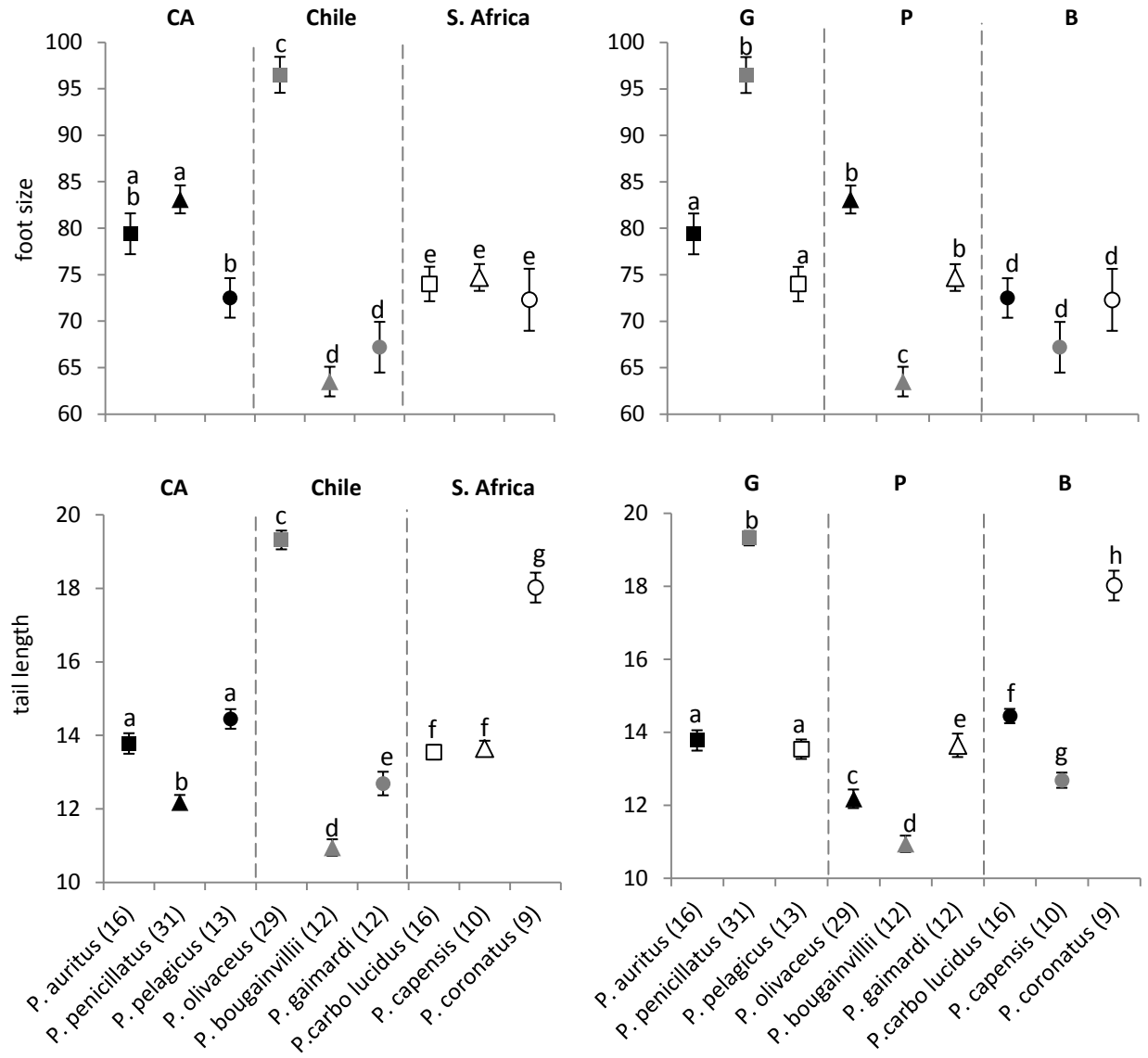






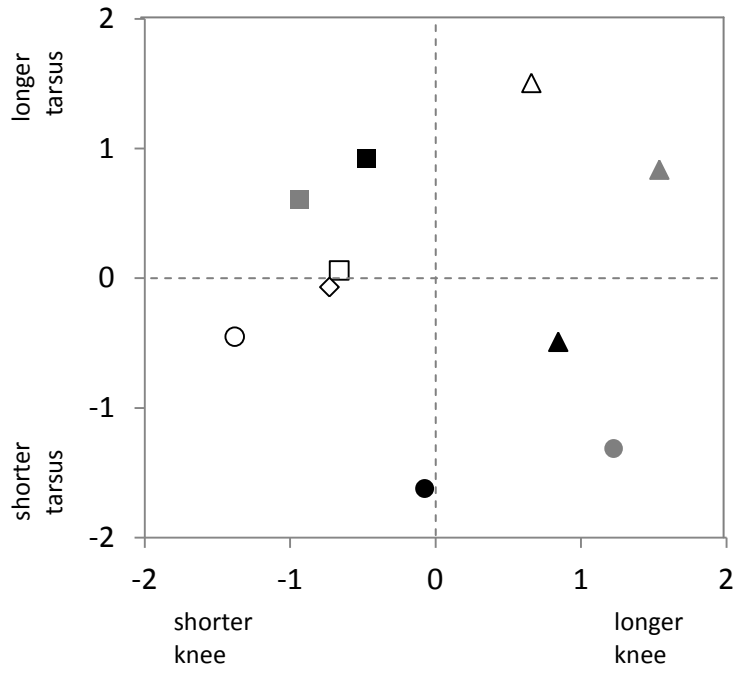
**Fig. 4**

Comparison of femur head diameter means  $\pm$  SE by region. Tukey HSD tests were used for comparisons within each region. Species with identical letters above were found to have similar body sizes. Squares, triangles, and circles represent generalist, pelagic and benthic feeders, respectively; rhomboid represents fourth S. African species, *P. neglectus*. Symbol color indicates region: black, grey, and white indicate California, Chile, and S. Africa, respectively. Sample sizes are given in parentheses.



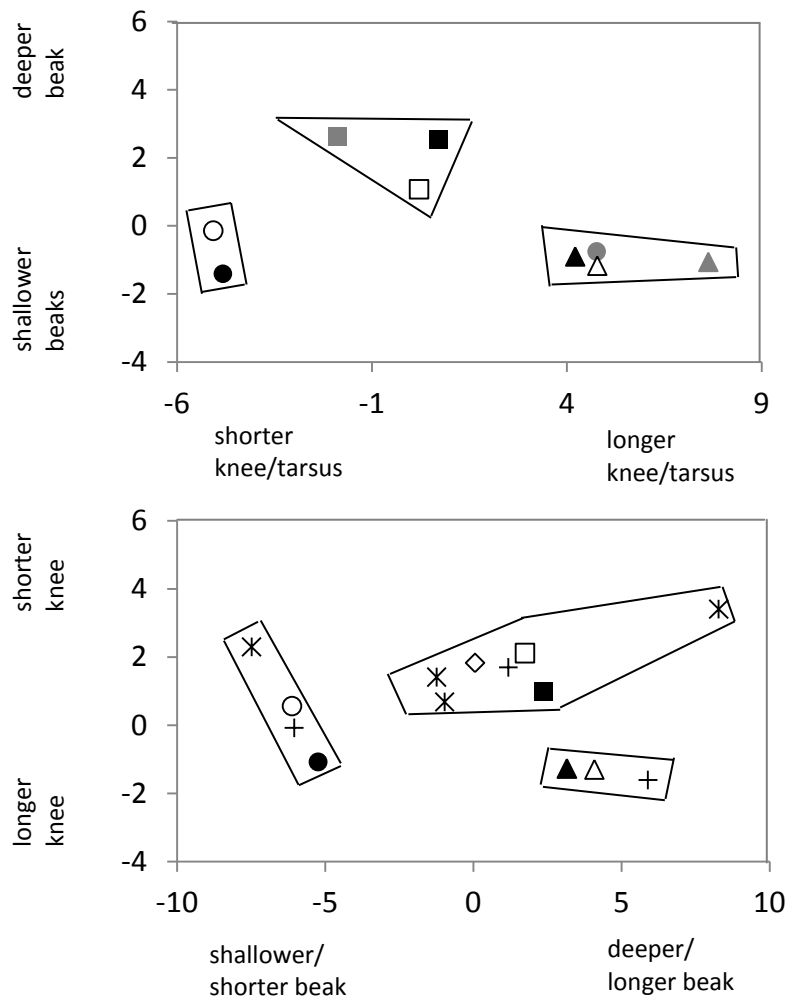
**Fig. 5.**

Foot sizes (top) and tail lengths (bottom) separated by region (left) and feeding type (right). Black, grey, and white symbols indicate species from California, Chile, and S. Africa, respectively. Squares, triangles, and circles indicate generalist, pelagic, and benthic feeding types, respectively. Numbers in parentheses indicate sample sizes.



**Fig. 6**

Principal Component Analysis species distributions along PC 1 and 2. Putative generalist, pelagic, and benthic feeders are represented by squares, triangles, and circles, respectively for the regions of California (black), central Chile (grey) and S. Africa (white). South Africa's *P. neglectus* is represented by a rhomboid.



**Fig 7.**

Top: Discriminate Function Analysis showing mean scores for each species. California (black) and S. African (white) species were used to create groups. Grey symbols indicate projected feeding counterparts from central Chile assigned by the analysis. Generalist, pelagic, and benthic feeders are represented by squares, triangles, and circles, respectively. Polygons indicate DFA groupings of species. Bottom: same as top but for non-phylogeny adjusted species. The rhomboid represents the fourth species from S. Africa, *P. neglectus*, that lacks counterparts in Chile and California. Crosses represent species from the Mediterranean Basin (MB), stars represent species from southwestern Australia. Species from the MB and Australia were assigned by the analysis.