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YELLOW-LEGGED GULLS FROM THE MEDITERRANEAN ARE NOT ONLY LARGER BUT ALSO ALLOMETRICALLY LONGER-WINGED THAN THOSE FROM THE CANTABRIAN-ATLANTIC

LAS GAVIOTAS PATIAMARILLAS DEL MEDITERRÁNEO NO SÓLO SON MÁS GRANDES QUE LAS CÁNTABRO-ATLÁNTICAS SINO QUE ADEMÁS TIENEN ALAS ALOMÉTRICAMENTE MÁS LARGAS

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Summary.—Variability in morphology and body size between populations of the same species is common and can be influenced by environmental conditions or differential migratory strategies. We focused on analysing body size differences between Yellow-legged gulls *Larus michahellis* from Mediterranean and Cantabrian-Atlantic Iberian colonies as previous studies have suggested that Cantabrian-Atlantic gulls are smaller than Mediterranean gulls. However, those analyses were based on small sample sizes or did not account for sexual dimorphism. Here we analyse an extensive biometric data set (> 1,500 adult individuals), separating males and females, from nine different sites in each region. Our results reveal a 7% (median) difference both between regions and sexes, for most morphometric variables, with Mediterranean gulls having longer legs (tarsi) and heads (cranium-bill) and thicker bills (bill-depth). This inter-regional difference was even larger for body mass, Mediterranean gulls being 11% (males) and 20% (females) heavier than Cantabrian-Atlantic gulls. In particular, we found that individuals from the Mediterranean populations were allometrically longer-winged than their northern counterparts. We suggest, after discarding other factors, that this wing allometry may be related to

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the sedentariness of the Cantabrian-Atlantic gulls, compared with the partially migratory strategy of Mediterranean gulls. We also suggest that the larger body size of Mediterranean gulls may help them compete better with resident gulls for food acquisition, once they coincide in the Cantabrian-Atlantic region. Finally, females from both populations were also found to be proportionately longer-winged than males. We hypothesise that this difference could allow smaller females to travel longer distances locally in search of food or to make use of different habitat types, avoiding foraging competition with the larger males.—Marcos Pacheco, M.L., Tavecchia, G., Igual, J.M., Alonso-Álvarez, C., Arizaga, J., Galarza, A., Oro, D. & Martínez-Abraín, A. (2023). Yellow-legged Gulls from the Mediterranean are not only larger but also allometrically longer-winged than those from the Cantabrian-Atlantic. *Ardeola*, 70: 225-240.

Key words: adaptation, allometry, biometry, migration, oceanographic conditions, sexual dimorphism.

Resumen.—La variabilidad en la morfología y el tamaño del cuerpo es común entre poblaciones de la misma especie y puede verse influenciada por las condiciones ambientales o por estrategias migratorias diferenciales. En este trabajo nos centramos en analizar las diferencias de tamaño corporal entre las gaviotas patiamarillas *Larus michahellis* del Mediterráneo y de las colonias ibéricas cántabro-atlánticas, ya que estudios previos sugirieron un tamaño más pequeño de las gaviotas del Cantábrico/Atlántico en comparación con las gaviotas mediterráneas. Sin embargo, esos análisis se realizaron empleando tamaños de muestra pequeños o no tuvieron en cuenta el gran dimorfismo sexual de la especie. Aquí, analizamos un extenso conjunto de datos biométricos (> 1,500 individuos adultos), separando machos y hembras, de nueve sitios diferentes en cada una de las dos regiones. Nuestros resultados revelaron una diferencia del 7% (mediana) tanto entre regiones como entre sexos, para la mayoría de las variables morfométricas, teniendo las gaviotas mediterráneas patas (tarsos) y cabezas (cráneo-pico) más largos y picos (altura de pico) más gruesos. Esta diferencia entre regiones fue aún mayor en el peso, siendo las gaviotas mediterráneas un 11% (machos) y un 20% (hembras) más pesadas que las gaviotas cántabro-atlánticas. Es importante destacar que los individuos de las poblaciones mediterráneas tuvieron alas alométricamente más largas que sus contrapartes del norte. Sugerimos que esta alometría alar puede estar relacionada con el sedentarismo de las gaviotas cantábrico-atlánticas, frente a la estrategia parcialmente migratoria de las gaviotas mediterráneas, tras descartar otros factores. También sugerimos que el mayor tamaño corporal de las gaviotas mediterráneas podría ayudarles a competir mejor con las gaviotas residentes por la adquisición de alimento, una vez coinciden en la región cántabro-atlántica. Finalmente, también se encontró que las hembras de ambas poblaciones tuvieron alas proporcionalmente más largas que los machos. Proponemos que esa diferencia podría permitir que las hembras (más pequeñas) viajen distancias más largas a nivel local en busca de alimento o hagan uso de diferentes tipos de hábitat, evitando la competencia de forrajeo con los machos más grandes.—Marcos Pacheco, M.L., Tavecchia, G., Igual, J.M., Alonso-Álvarez, C., Arizaga, J., Galarza, A., Oro, D. y Martínez-Abraín, A. (2023). Las gaviotas patiamarillas del Mediterráneo no sólo son más grandes que las cántabro-atlánticas sino que además tienen alas alométricamente más largas. *Ardeola*, 70: 225-240.

Palabras clave: adaptación, alometría, biometría, condiciones oceanográficas, dimorfismo sexual, migración.

Introduction

In any large population of animals or plants, variability in the expression of individual features is the rule (Albert *et al*., 2011; Koppik *et al.,* 2015) and the basis of evolution by natural selection (Violle *et al*., 2012). We can only expect little variability and fixed traits due to genetic drift in small populations (De Rochambeau *et al*., 2000). Among individual animal features more commonly influenced by environmental factors is the evolution of adaptive variability in body size (Smith *et al*., 2018).

Regarding the Yellow-legged Gull *Larus michahellis*, taxonomists have described two different subspecies, based on expert opinion, on the basis of apparent morphological differentiation between the Iberian populations distributed along the Mediterranean coast, the Gulf of Cádiz and the Chafarinas Islands *L. m. michahellis* (Naumann, 1840), and *L. m. lusitanius* (Joiris, 1978) and those resident on the Cantabrian-Atlantic coast, extending from Galicia to the Basque Country (and Portugal). A third subspecies, *L. m. atlantis* (Dwight, 1922), has been assigned to the Canary Islands, Madeira and the Azores (Macaronesia) (Pons *et al*., 2004; Arizaga *et al*., 2009; Bermejo *et al.,* 2009).

More recently, Mínguez & Ganuza (1995) suggested that Cantabrian-Atlantic gulls are smaller than Mediterranean gulls, although working with small sample sizes and not accounting for the confounding factor represented by the large sexual dimorphism present in this species. More specifically, these authors reported that Yellow-legged gulls from the Basque Country were slightly smaller than those from Galicia, but that both Cantabrian-Atlantic populations were much smaller than Mediterranean gulls (with data taken from Carrera *et al*., 1987 from the Medes and Chafarinas Islands). In turn, gulls from different Mediterranean colonies did not differ in all variables compared.

Subsequently Pons *et al*. (2004) reported an overall smaller body size for Atlantic Iberian populations (Basque Country and Galicia), and those from the Camargue in the French Mediterranean, again working with relatively small sample sizes, although including individuals of both sexes. Pons *et al*. (2004) aimed to show that Iberian Atlantic gulls did not show stronger signs of introgression with the Herring Gull *Larus argentatus*, whose small size resembles that of Iberian Atlantic gulls, relative to other populations of Yellow-legged gulls, rather than demonstrating biometric differences between populations.

The availability of food resources is among the main environmental factors influencing morphological differences between populations of the same species in seabirds (Iapichino *et al*., 1983; Granadeiro, 1993). The availability of food per capita is often what matters most, rather than just food availability, since density dependence operates (Wootton, 1997; Pedrocchi *et al*., 2002). Thus, morphological differences between Cantabrian-Atlantic and Mediterranean Yellow-legged Gull populations could be related to the well-known differences in productivity between the two seas (Goffredo & Dubinsky, 2013). On that basis, the Cantabrian-Atlantic gulls would be expected to be larger than the Mediterranean ones unless densities have been unequal in both regions.

In addition, a likely differential consumption of anthropogenic food subsidies could have favoured body size differences (e.g. Oro *et al*., 2013). Opportunistic gull species *Larus* spp. commonly benefit from this type of food (see, e.g. Real *et al*., 2017), basing their diet mainly on garbage and fishing discards, consuming self-caught fish to a lesser extent. This type of foraging habit fosters their presence in anthropic environments, where they make intense use of open-air landfills (Fossi & Renzoni, 1989; Duhem *et al.,* 2003; Jordi *et al.,* 2014) and also follow fishing boats (Oro *et al*., 1999; Martínez-Abraín *et al*., 2002a). Gulls using Predictable Anthropogenic Food Sources (i.e. PAFS) would be expected to be larger than those that do not use them (Genovart *et al*., 2010; Oro *et al*., 2013).

Other than food, variation in flight frequency or migration distance could also influence morphological and body size differentiation. This effect could promote differences between populations and also between sexes within the same population. In this regard, morphological variation in wing length has long been related to the migratory habits of birds (Hamilton, 1961). Longer wings are more important when travelling long distances; thus, migratory species tend to have proportionally longer wings than resident species (Pilastro & Spina, 1997; Böhning-Gaese*et al*., 2003; Forschler & Bairlein, 2011; Ponti *et al*., 2018).

We conducted a large-scale comparative study to test the reliability of the previously reported biometric differences between Cantabrian-Atlantic and Mediterranean populations of the Yellow-legged Gull, using for the first time a large data set and accounting for the sexual dimorphism of the species (Bosch, 1996; Pons *et al*., 2004). We thus avoided biased comparisons between populations. We expected to confirm the differences previously reported in the literature, despite their being counter-intuitive, since they oppose the food availability differences between the two study regions. We aimed to suggest possible adaptive explanations for the expected differences between regions, which could be tested in future studies when appropriate data are available. More specifically, we expected to find morphological signatures reflecting the resident (Cantabrian-Atlantic) versus the partially-migratory (Mediterranean) character of the study populations (Pons *et al*., 2004), assuming differences are adaptive in some way.

Materials and methods

Variables

We used datasets with biometric information from adult Yellow-legged gulls from non-consecutive trapping campaigns carried out in several Cantabrian-Atlantic and Mediterranean colonies between 1994 and 2020. More specifically, the data come from four different autonomous regions: two Cantabrian-Atlantic (Galicia and Basque Country) and two Mediterranean (Balearic Islands and Catalonia), and 18 colonies (nine in the Cantabrian-Atlantic region and nine in the western Mediterranean) (Tables S1 and S2). All the information was compiled in a single database containing the following variables: individual, sex, colony, region, year, wing length, tarsus length, cranium-bill, bill depth and weight. The individuals from which measurements were taken were numbered, 1 to 1,562. Individuals were recorded as male (1) or female (2). Of the total number of individuals, 673 were males (372 from the Cantabrian-Atlantic region and 301 from the Mediterranean region), 641 were females (408 from the Cantabrian-Atlantic and 233 from the Mediterranean), and 248 were not sexed (65 from the Cantabrian-Atlantic and 183 from the Mediterranean). Each individual was assigned a number from 1 to 16 to indicate their colony of origin (Table S2). Individuals were classified according to their region of origin, assigning 1 to individuals from the Cantabrian-Atlantic (845 individuals) and 2 to those from the Mediterranean (717 individuals). The year in which the measurements of each individual were taken was recorded but not used since these were different for each colony and not taken in consecutive years in most cases (Table S1). In any case, we were interested in performing just spatial analysis, assuming constancy over time in biometric differences. Wing length was recorded as the maximum chord, with the wing flattened and stretched against the ruler. Tarsus Length measurements included the tibia-tarsus joint; i.e. with the calliper rested on the back of the joint with the leg flexed. Cranium-Bill measurements were the distance between the back of the skull and the bill tip. Bill Depth was measured at its widest point, at the red bill spot. All measurements collected in the database were recorded to the nearest millimetre. Weigh was measured in grams, with dynamometer precision ranging between 5, 10 and 20g among colonies.

Statistical analyses

An initial descriptive study was carried out by estimating the arithmetic mean and standard deviation of each variable, separating by sex and region (Table S3), and also calculating the percentage differences, between sexes and regions, for each variable considered. Boxplots were generated (in SPSS version 27) for each variable studied, obtaining a grouped visual representation of the differences. Once the descriptive analysis of the data was completed, we proceeded to the statistical contrast of null hypotheses (inferential phase) using the R software environment (https://www.r-project.org/).

Normality tests were carried out for all variables. The distribution of each of these variables was studied using Shapiro tests. A logarithmic transformation (log10) was carried out to minimise the effects caused by the lack of normality in the distribution of some of the variables analysed. Bartlett's tests for the homogeneity of variances were also conducted for each variable. Once normality and homogeneity of the variances for each variable had been analysed and, based on the Central Limit Theorem, in those cases where normality was not attained even after log transformation, contrasts of population means were carried out for variables with homogenous and non-homogenous population variances using ANOVA and t-tests for unequal variances respectively. We also carried out correlation analyses (Pearson's r) between all the studied variables, building correlation matrices.

A new variable named Raio was generated which weighted Wing-Length by the structural variable selected (Cranium-Bill), to test for wing allometry by sex and region. Specifically, Wing Length was divided by Cranium-Bill to obtain the Ratio variable. The decision to use Cranium-Bill to represent body size, instead of tarsus length, was based on the strong correlation between these two variables. Also, according to our field experience, tarsus length measurements can differ more between measurers than cranium-bill. Moreover, discriminant functions developed for Yellow-legged gulls indicate that the cranium-bill measurement is an essential variable for sexing this species (Bosch, 1996; Galarza *et al*., 2008).

To analyse wing allometry, a generalised linear model (GLM) with an interaction term between sex and region (Ratio~Sex*Region) was specified, using the heavyLm function of the heavy library of R and a Cauchy distribution of errors, appropriate for modelling the ratio of two normal variables. This model allowed us to test whether there were differences in the ratio between sexes and between regions, and also whether or not the ratios differed between sexes in each region. Boxplots were built to visually compare the new variable Ratio for both sexes and regions.

Results

Descriptive results

Most variables did not pass the normality test, except for Bill Depth for both sexes and regions (Table S4). The results of Bartlett's tests for the homogeneity of variances showed that approximately half the variables considered showed homogeneity between population variances and half did not (Table S5).

The descriptive study of the variables showed that, on average, Mediterranean gulls (regardless of sex) were larger (i.e. had higher median values) than Cantabrian-Atlantic gulls (Figure 1; Table S3). We also found that, on average, males had a larger body size than females, regardless of region (Figure 1; Table S3).

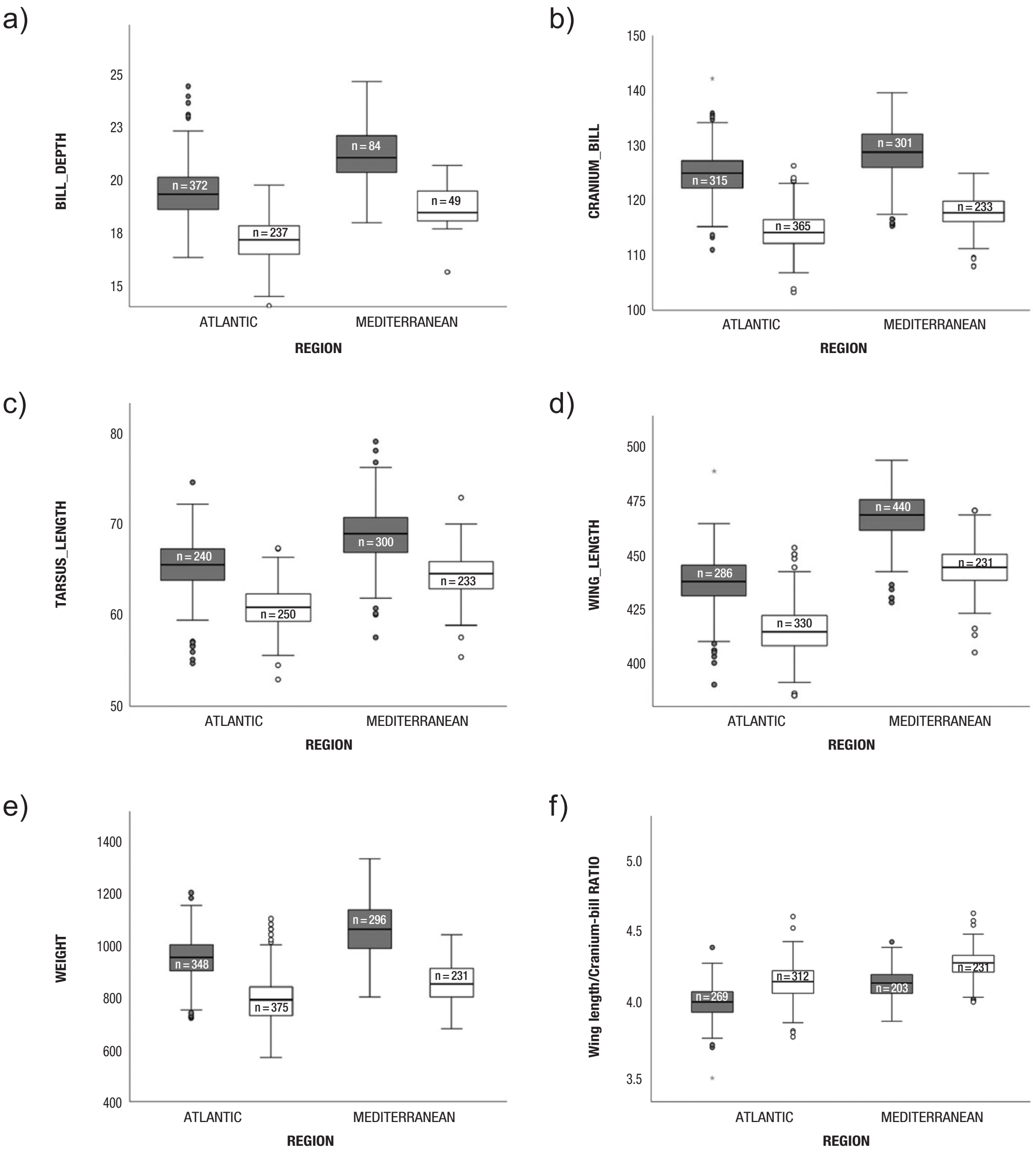

FIG. 1.—Boxplots comparing a) Bill Depth (mm), b) Cranium-Bill (mm), c) Tarsus Length (mm), d) Wing Length (mm), e) Weight (g) and f) Wing length/Cranium-bill Ratio of Cantabrian-Atlantic and Mediterranean Yellow-legged gulls (Males: grey boxes; Females: white boxes). Dots are outliers and asterisks represent extreme values. Boxplots depict medians (50%), interquartile intervals (25% and 75%) and ranges (maximum and minimum).

[Diagramas de caja que comparan a) Altura del pico, b) Cráneo-Pico, c) Longitud del tarso, d) Longitud del ala, y e) Peso y f) Ratio Ala/Cráneo-Pico de gaviotas patiamarillas del Cantábrico-Atlántico y del Mediterráneo (Machos: cajas sólidas grises; Hembras: cajas sólidas blancas). Los puntos sólidos son valores atípicos y el asterisco representa valores extremos. Los diagramas de caja representan la mediana (50%), el intervalo intercuartílico (25% y 75%) y el rango (máximo y mínimo).]

Hypothesis testing and quantification of differences

Our inferential analyses showed statistically significant differences between the means of all variables for both sexes and regions (Table 1). Based on these results, we quantified the percentage difference between sexes within and between regions. Considering all variables together (except for Weight), the median magnitude of the differences between regions for both sexes was 7%, the same as the median differences between males and females within the same region (Figure 2). Weight differences were much larger, with Mediterranean females being almost 20% heavier than Cantabrian-Atlantic females, and Mediterranean males 11% heavier than Cantabrian-Atlantic males. In both regions males were nearly 20%

TABLE 1

Results of the statistical contrast of arithmetic means for all study variables using ANOVA tests or Student-t tests (with unequal variances between populations). CA: Cantabrian-Atlantic; MED: Mediterranean.
[Resultados del contraste estadístico de medias aritméticas para todas las variables de estudio mediante pruebas ANOVA o pruebas t de Student (con varianzas desiguales entre poblaciones). CA: Cantábrico-Atlántico; MED: Mediterráneo.]

	Males CA	**Females MED**
	BILL DEPTH	
Females CA	F = 14.16 (< 0.05)	F = 6.04 (< 0.05)
Males MED	F = 47.21 (< 0.05)	F = 114.7 (< 0.05)
	CRANIUM-BILL	
Females CA	F = 421.5 (< 0.05)	F = 226.1 (< 0.05)
Males MED	t = −10.28 (< 0.05)	t = 23.4 (< 0.05)
	TARSUS LENGTH	
Females CA	F = 151.5 (< 0.05)	t = −16.1 (< 0.05)
Males MED	t = −13.02 (< 0.05)	F = 251.3 (< 0.05)
	WING LENGTH	
Females CA	t = 20.71 (< 0.05)	F = 991.3 (< 0.05)
Males MED	t = −26. 407 (< 0.05)	F = 564.6 (< 0.05)
	WEIGHT	
Females CA	t = 25.62 (< 0.05)	t = −14.87 (< 0.05)
Males MED	t = −7.07 (< 0.05)	t = 13.38 (< 0.05)

heavier than females. Hence, the weight difference between females from each of the two regions was of the same magnitude as the differences between males and females within regions (20%). In general, interregional differences were of larger magnitude for females than for males in all variables, except for Wing Length in which case differences were equal for both sexes (5.5%). The magnitude of the differences in Wing Length between males and females was also similar within both regions (6.9%), although larger than the differences in this trait between regions for both sexes (5.5% vs 6.9%).

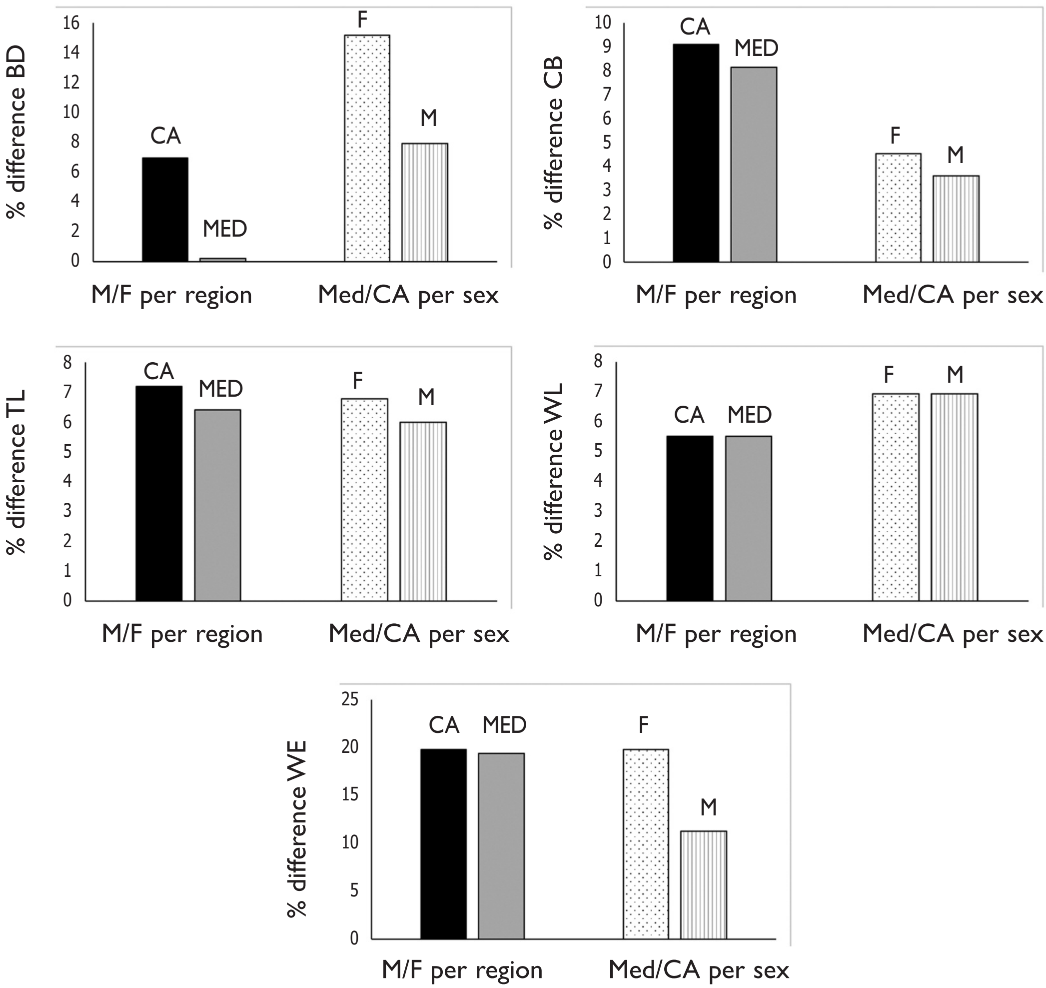

FIG. 2.—Percentage differences in Bill Depth (BD), Cranium-Bill (CB), Tarsus Length (TL), Wing Length (WL) and Weight (WE) between sexes in each region and between regions for each sex. MED: Mediterranean region; CA: Cantabrian-Atlantic region; M: Male gulls; F: Female gulls.
[Diferencias porcentuales en Altura del pico (BD), Cráneo-Pico (CB), Longitud del tarso (TL), Longitud del ala (WL) y Peso (WE) entre sexos en cada región y entre regiones para cada sexo. MED: Región Mediterránea; CA: Región Cantábrico-Atlántica; M: Gaviotas macho; F: Gaviotas hembras.]

The smallest difference between regions corresponded to Cranium-Bill both for males and females (3.60% and 4.53%).

Wing-length allometry in relation to body size

The generalised linear model with interaction term fitted for Ratio identified statistically significant sex and regional effects on wing allometry (Table 2). However, no statistically significant interaction between both factors was found, indicating that Ratio did not vary differently between sexes according to region. Females had a median Ratio larger than males, and Mediterranean individuals had a median Ratio larger than Cantabrian-Atlantic individuals (Figure 1f).

CRANIUM-BILL had a statistically significant strong and positive correlation with Tarsus Length for both sexes in both regions (Table S6). Tarsus length is another alternative variable typically used to represent body size. This strong correlation confirms that the cranium-bill measurement is a good proxy of the general body size of individuals of both sexes, as is tarsus length.

Discussion

Differences between populations

Our study has confirmed that, after accounting for sex and with a large and balanced data set, Yellow-legged gulls from the Mediterranean populations are indeed larger than those from Cantabrian-Atlantic populations. This supports earlier studies in which the same differences in body size were reported (Mínguez & Ganuza, 1995; Pons *et al*., 2004). Our results were compared to those reported by Pons *et al*. (2004) for Mediterranean and Atlantic Yellow-legged gulls (using much smaller sample sizes) and were found to be quite similar.

Likely causes of the differences

The Mediterranean Sea is oligotrophic compared to the Cantabrian-Atlantic region due to its self-cleaning mechanism driven by the outgoing bottom drainage at the Straits of Gibraltar (Krom *et al.,* 1991; Zotier *et al*., 1999). In addition, the oceanographic condi-

Table 2

Results of modelling the variable Ratio by means of Generalised Linear modelling with a Cauchy distribution of errors. SE: Standard Error; d. f.: Degrees of freedom.
[Resultados de la modelización de la variable Ratio mediante Modelos Lineales Generalizados con distribución de errores Cauchy. SE: Error estándar; d.f.: Grados de libertad.]

	Estimate	**SE**	**Z**	**p-value**
Intercept	1.2399	0.0009	1325.87	0.0000
SEX	0.0104	0.0006	17.90	0.0000
REGION	0.0097	0.0006	15.70	0.0000
SEX*REGION	−0.0001	0.0004	−0.17	0.8664

d.f: 1022 total; 1018 residual
Log-likelihood: 3349.01 on 5 d.f.

tions of the Mediterranean Sea are characterised by the development of a summer thermocline that causes a substantial drop in primary productivity (Rodríguez, 1982), which can affect both adults and fledglings of the Yellow-legged Gull. In contrast, the predominance of upwellings and large intertidal surfaces where food is abundant (Le Mao & Yesou, 1993) make the Cantabrian-Atlantic coasts rich in primary and secondary productivity. However, the marked climatic and oceanographic differences between the Cantabrian-Atlantic and Mediterranean regions cannot be the main factor influencing the remarkable phenotypic differences found, because one would have expected a larger body size in the more productive region, whereas the pattern found was the converse.

Seabirds, and especially gulls, often resort to trophic resources of anthropogenic origins, such as landfills or discards from fishing activities (Bertellotti *et al.,* 2001; Duhem *et al*., 2005; Ramos *et al.,* 2009; Granadeiro *et al.,* 2014; Real *et al*., 2017). The predictability of discards derived from landfills and fishing activities may encourage a greater preference for this type of food source than for natural food sources (Bosch *et al*., 1994; Bertellotti *et al*., 2001). Mammal studies have shown that individuals with access to solid waste dumps (greater availability of food in PAFS) had larger average body sizes (see Oro *et al*., 2013). Similarly, Auman *et al*. (2008) found that Silver Gulls *Chroicocephalus novaehollandiae* feeding on dumps and urban wastes were larger than those feeding on more natural resources. Nevertheless, both Yellow-legged Gull populations have extensively used landfills and fishing discards in the past (Ramos *et al*., 2009; Arizaga *et al*., 2013), and hence anthropogenic food availability should not have determined the differences.

It is also necessary to consider that food availability is influenced by density dependence, i.e. the number of birds in each region competing for access to food (see, e.g. Ruiz *et al*., 1998). Thus, it could be postulated that Cantabrian-Atlantic gulls are smaller, despite inhabiting a more productive sea because the food per capita they get is lower due to higher gull densities. However, before culling was performed in Mediterranean colonies, and major landfills were closed in both regions (around the same time), inter-regional densities of gulls were similar, with ca. 25,000 pairs at the main western Mediterranean colony (Medes Islands) (Bosch *et al*., 2000) and ca. 22,000 pairs at the main Atlantic colony (Cies Islands) in the 1990s (Munilla *et al*., 1991). Therefore, differential gull density in both regions does not explain the smaller body size of Cantabrian-Atlantic gulls either.

Hence, after discarding other alternative options, we postulate that the differences found may have to do with the differential sedentariness of both populations. Several studies have shown that Iberian populations in the Cantabrian-Atlantic region are mostly resident, with only a small fraction, mainly juveniles or immatures (Munilla, 1997; Sol *et al.,* 1995), making movements out of their places of origin (Arizaga *et al*., 2010). In contrast, the Mediterranean populations are mainly migratory, frequently moving to the Cantabrian-Atlantic region after breeding (Munilla, 1997; Martínez-Abraín *et al*., 2002b; Rodríguez & Muntaner, 2004; Arizaga *et al.,* 2009b; Galarza *et al*., 2012). Temporal instability in the availability of food resources is one of the main causes promoting migration (Newton, 2008), and this fact could explain why individuals from less productive Mediterranean regions migrate towards the Cantabrian-Atlantic coasts of the Iberian Peninsula after breeding, where trophic resources are more abundant and stable over time (Incarbona *et al*., 2010).

This difference in migratory behaviour between the two regions could explain the difference in wing-length vs body size allometry detected in our study. That difference may be a morphological adaptation of Mediterranean populations (longer-winged) to their longer displacement requirements. The theory of aerodynamics predicts that proportionally long wings are the most efficient trait for extended flights (Norberg, 1995). Studies on several species postulate a positive intraspecific relationship between migration distance and body-size-controlled wing length (Pilastro & Spina, 1997; Forschler & Bairlein, 2011). It seems reasonable to argue that gulls that travel long distances during their migration have proportionally longer wings than resident gulls, a hypothesis supported studies that detected an 8% increase in wing length in migratory populations of Eurasian Blackcap *Sylvia atricapilla* compared to sedentary populations (Pérez-Tris & Tellería, 2001). We suggest an adaptive meaning of the wing allometry detected between gull populations from the two regions. Explaining why Mediterranean gulls are larger than Cantabrian-Atlantic gulls in biometric variables unrelated to flight efficiency is less easy.

We postulate that overall bigger body size could help individuals from Mediterranean populations to be better competitors once in the Cantabrian-Atlantic region (Almaraz & Oro, 2011). Considering that resident gulls have better knowledge of local resources, having a body size advantage could increase survival in an unfamiliar oceanographic environment and in an unfavourable social environment. However, this remains speculative until some empirical demonstration is provided.

It is interesting that the magnitude of the differences detected for all variables (except for weight) oscillated around a constant value of 7%, quite similar to the 8% reported by Pérez-Tris & Tellería (2001) for Blackcaps. We suggest that the 7% difference could represent a threshold, a product of biological constraints, in body size change across species that may allow higher flight efficiency or provides some competitive advantage. This threshold value can be useful for future biometric comparisons between *Larus* gull populations, because it could be used to develop informed null hypotheses (instead of 'no effect' null hypotheses) using *a priori* power tests within the frequentist paradigm or could be taken as priors in Bayesian analyses. The magnitude of these differences cannot be due simply to measuring differences among researchers between populations, as the precision of digital callipers used was 0.01mm and that of rulers 1mm. In addition, weight differences, between populations and sexes, were as large as 20% (ca. 100g), which cannot be accounted for by the fact of having used dynamometers with variable precision (5g, 10g and 20g) among colonies. The fact that females had larger differences than males between regions in most traits can be due to wider window of potential variability for the smaller sex if there are upper limitations for body size: i.e. males would be closer to that upper limit. The constancy in Wing Length differences between sexes and regions suggests some type of stronger biological constraint on the variability of this trait compared to the others studied.

Differences between sexes

Although the main aim of our analyses was to confirm body size differences between regions, accounting for sex differences, our results also confirm previous findings regarding large sexual dimorphism both for Mediterranean gulls (Bosch, 1996) and Basque Country gulls (Arizaga *et al*., 2008; Galarza *et al*., 2008) and quantify the differences (large and similar between regions). At the intra-population level, body size variation in mammals and birds has been previously interpreted as the result of phenotypic changes due to natural or sexual selection (Clutton-Brock, 2004).

Our finding that females from both populations were proportionally longer-winged than males could represent an adaptive response to avoid inter-sexual competition in foraging (see e.g. García-Tarrasón *et al*., 2015 in relation to Audouin's Gull *Ichthyaetus audouinii*). Smaller females could be forced to perform longer displacements locally to obtain food for the chicks due to larger territorial males displacing females from foraging sites closer to breeding colonies or making use of different foraging habitats in which a longer wing could result advantageous. This evolutionary pressure is well exemplified in terms of body size in raptors with marked sexual dimorphism: e.g. the Northern Goshawk *Accipiter gentilis*, the Eurasian Sparrowhawk *Accipiter nisus* and the Peregrine Falcon *Falco peregrinus,* in which females, which are larger, have access to better food resources. As a by-product of this, males and females end up providing chicks with a more diverse diet (Panter & Amar, 2021). Results of studies that examined several *Larus* gulls species support our results, as they show that *Larus* gulls males generally have proportionally longer and more robust beaks, but proportionally shorter wing lengths than females (i.e., Ingolfsson, 1969).

Comparative studies on cumulative flight distances between resident and migratory populations, flight efficiency and foraging competition between sexes and between gulls from both regions should be performed when suitable data become available in the future, to test our hypotheses.

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Table S1. Origin, team members, geographical location and year of the biometric measurements used in this study.
[Origen, equipo, ubicación geográfica y año de las medidas biométricas utilizadas en este estudio.]

Table S2. The number of study colonies and adult Yellow-legged gulls measured per colony.
[Número de colonias de estudio y gaviotas patiamarillas adultas medidas por colonia.]

Table S3. Means and standard deviations (SD) of all study variables for males and females from both regions.
[Media y desviación estándar (DE) de todas las variables de estudio para machos y hembras de ambas regiones.]

Table S4. Results of the analysis of normality (Shapiro tests) for all study variables. CA: Cantabrian-Atlantic; MED: Mediterranean.
[Resultados del análisis de normalidad (pruebas de Shapiro) para todas las variables de estudio. CA: Cantábrico-Atlántico; MED: Mediterráneo.]

Table S5. Results of the analysis of the homogeneity of the variances for all variables. CA: Cantabrian-Atlantic; MED: Mediterranean.
[Resultados del análisis de homogeneidad de las varianzas para todas las variables. CA: Cantábrico-Atlántico; MED: Mediterráneo.]

Table S6. Correlation matrices (Pearson's r) among study variables for males and females from both study regions.
[Matrices de correlación (r de Pearson) entre variables de estudio para machos y hembras de ambas regiones de estudio.]

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