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Spatial variation in egg size of a top predator: Interplay of body size and environmental factors?

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ABSTRACT

It is expected that nearby populations are constrained by the same ecological features shaping in turn similarity in their ecological traits. Here, we studied the spatio-temporal variability in egg size among local populations of the critically endangered Balearic shearwater *Puffinus mauretanicus*, a top marine predator endemic to the western Mediterranean region. Specifically we assessed whether this trait was influenced by maternal body size, as an indicator of a genetic component, and feeding ecology (through stable-carbon and nitrogen-isotope measurements), as an indicator of environmental factors. We found that egg size varied among local populations, an unexpected result at such a small spatial scale. Body size differences at the local population level only partially explained such differences. Blood isotope measurements also differed among local populations. Values of $\delta^{15}\text{N}$ suggested inter-population differences in trophic level, showing a similar general pattern with egg size, and suggesting a nutritional link between them whereby egg size was affected by differences in feeding resources and/or behaviour. Values of $\delta^{13}\text{C}$ suggested that local populations did not differ in foraging habits with respect to benthic- vs. pelagic-based food-webs. Egg size did not vary among years as did breeding performance, suggesting that a differential temporal window could affect both breeding parameters in relation to food availability. The absence of a relationship between breeding performance and egg size suggested that larger eggs might only confer an advantage during harsh conditions. Alternatively parental quality could greatly affect breeding performance. We showed that inter-population differences in egg size could be influenced by both body size and environmental factors.

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1. Introduction

The study of variation in trait values among populations has received attention in recent years (Schluter et al., 2004; Duponchelle et al., 2000; Ruttenberg et al., 2005). Comparative investigation of trait values among populations is a powerful tool to understand selective factors that influence their ecological adaptation, spatial variability and evolution (Weimerskirch, 2002). Most studies examining patterns and processes in inter-population variation have been done over large spatial scales, and these variations are usually responses to differences in local environmental conditions (Schluter et al., 2004; Ruttenberg et al., 2005). However, across small geographic scales comparisons are limited to nearby populations (cf. Ruttenberg et al., 2005), and trait values are expected to be similar owing to the constraints imposed by similar ecological features.

Egg size has been widely studied because of its high variability (Hipfner, 2000), which in turn often varies widely within species, and is a representative trait of maternal breeding effort (Bernardo, 1996). Females could regulate their reproductive investment by controlling the number of eggs laid and/or their size. In the case of one egg clutches, females can only adjust their reproductive investment by breeding intermittently or by altering size or composition of eggs. Thus, single egg clutches are ideal systems to study potential factors affecting egg size (Weidinger, 1996). Within seabirds, this is the case for the order of the Procellariiformes, which lay a single egg each breeding attempt (Warham, 1990). For seabirds, egg size can also reflect environmental factors such as weather, oceanographic conditions, and marine resource availability around the colony during breeding (Oro, 1996; Michel et al., 2003).

Individual parental factors could also play an important role in egg size determination such as parental quality and body size. Egg size may increase to a threshold value associated with parental quality (e.g. age and breeding experience, see Brooke, 1990; Michel et al., 2003; Sagar et al., 2005). When egg size increases with maternal body size (Michel et al., 2003) a genetic component may be involved in egg size determination, although this relationship is not always clear within birds in general (Christians, 2002) and Procellariiformes in particular (Mougin, 1998). Finally, environmental and parental factors are not mutually exclusive and effects of environmental stochasticity on breeding performance may depend on the quality of the parents (Saether et al., 1997). For instance, lower mass at fledging would reduce the probability of survival until breeding (Weimerskirch et al., 2001). Egg size could also have important consequences on fitness-related traits such as increased hatching mass (Hipfner, 2000), chick size in the 1st week after hatching (Christians, 2000), rate of post-hatching development (Hipfner, 2000; Quillfeldt and Peter, 2000), and consequently reproductive success (Michel et al., 2003).

In this article, we investigated egg size variation in different local populations of the critically endangered Balearic shearwater *Puffinus mauretanicus*. The species is endemic to the Balearic archipelago, with a small breeding population (less than 2000 pairs and maximum distance between local

populations of ~160 km) (Ruiz and Martí, 2004). We assessed (1) the spatio-temporal variability of egg size in a relatively small geographical area, as well as the influence of (2) maternal body size and (3) feeding ecology in egg size variability, as potential indicators of genetic and environmental components respectively. As egg size could have important fitness consequences, we considered (4) the potential effect of egg size on breeding performance, as measured by hatching and breeding success. At such small spatial scale, we predicted that local populations should be affected similarly by predominant ecological features, and in turn show similar mean egg size. This should be especially true for our study populations, since they share physical and environmental features at their breeding sites (see Louzao et al., 2006a) that are potential determinants of variation in trait values at small spatial scale (e.g. Genovart et al., 2003b). Furthermore, most feeding birds concentrate on very few foraging grounds (i.e., the Ebro Delta and its area of influence, since it is biologically the most productive area) in the western Mediterranean (see Ruiz and Martí, 2004; Louzao et al., 2006b and references therein). Thus, within this oceanographic context nearby colonies could share foraging grounds at the population level due to the environmentally stable character of the Mediterranean ecosystem. Therefore, we did not expect egg size differences among local populations since egg size depends at least partially on feeding resources.

2. Materials and methods

2.1. Species and study area

The Balearic shearwater is a medium-sized (ca. 500 g), and slightly dimorphic Procellariiform, with males about 5% larger than females (Genovart et al., 2003a). Females lay a single egg that both parents incubate during 48–52 days, and the chick-rearing period extends ca. 65–70 days (Oro et al., 2004; Ruiz and Martí, 2004). The species is specialised at foraging on shoals of small pelagic fishes, although a bioenergetics model estimated that over 40% of the energetic demands of the total population was met by trawling discards during the breeding season at its main foraging ground, the eastern Iberian Peninsula (Arcos and Oro, 2002). However, Balearic shearwater distribution at mid and large scales does not seem conditioned by trawlers, suggesting that discards represents an “opportunistic” foraging resource when this fishery operates within their foraging grounds (Louzao et al., 2006b). During the breeding season, shearwaters are present in shallow shelf and coastal waters characterised by frontal systems in areas close to the breeding sites on the Iberian continental shelf, but other areas within the foraging range of the species could be important foraging areas such as the Balearic archipelago or Algerian coast (North Africa) (Ruiz and Martí, 2004; Louzao et al., 2006b). After breeding, Balearic shearwaters migrate to other areas of the Mediterranean or pass through the Strait of Gibraltar, surrounding the Iberian Peninsula, reaching the south of Great Britain and west of France (Ruiz and Martí, 2004). After returning to the Mediterranean, birds also concentrate in the eastern Iberian Peninsula during the pre-breeding

season, but with a more coastal and aggregated distribution, and foraging mainly on small pelagic fishes (Arcos, 2001, 2005).

Fieldwork was conducted at three local breeding populations from Mallorca and Menorca islands: Sa Cella (39° 36' N, 2° 22'; noted by CEL), and Conills (39° 30' N, 2° 28' E; noted by CON) in Mallorca, and Mola de Maó (39° 53' N, 4° 19' E; noted by MOL) in Menorca through the 2001–2004 breeding seasons (Fig. 1). In the three study sites, breeding population ranged from ca. 45 pairs (CON) to ca. 200 pairs (CEL and MOL). Habitat features were similar in all studied colonies (i.e., clay soil and protected nests) and they were located in deep caves (CEL), between alluvia in coastal cliffs (MOL) and islets (CON), and only MOL was accessible by land. Local populations within Mallorca were separated ~15 km and between Mallorca and Menorca maximum distance was ~160 km.

2.2. Field procedures: egg measures, breeding performance and adult sampling

Since the species breeds synchronously, local populations were visited simultaneously through the incubation period (from late February to late April) and all accessible active nests (i.e., nests where a current-year egg was found) were marked. We measured the total egg length and breadth to the nearest 0.01 mm with a digital calliper. Egg size was estimated as an egg volume index (in cm^3) = $0.00051 \times \text{egg length} \times (\text{egg breadth})^2$ (Hoyt, 1979). We collected information on 349 eggs from three local populations of Balearic shearwaters ($n = 265, 45$ and 37 at CEL, CON and MOL respectively). Mean (\pm SE) egg size (in cm^3) ranged from 51.99 ± 1.22 to 58.64 ± 1.07 (Figs. 1 and 2). Visits were repeated in mid May and June to record hatchlings and fledglings, respectively, at each monitored nest. Hatching and breeding success (as the percentage of hatchlings and fledglings by eggs laid, respectively) were estimated only in local populations from CEL and CON,

since MOL was only visited during the incubation period. We assessed hatching and breeding success from 263 and 259 breeding attempts (measured eggs), respectively. Hatching and breeding success ranged between 0.75–1 and 0.68–1, respectively, in both local populations from Mallorca (see Louzao et al., 2006a for more details in breeding performance). Owing to logistic and natural constrains (i.e., time and accessibility, as well as no breeding attempts in specific years during the 4-year study period) we were not able to monitor the same nests in each local population annually. These types of limitations occur when studying species of high conservation concern, such as the critically endangered Balearic shearwater, since monitoring requires maximum caution.

We captured adult breeders (identified when incubating or attending a young chick in the nest) and took morphological measurements only once (head plus bill length, bill depth at nostrils, and tarsus with a digital calliper to the nearest 0.01 mm) (see Table 1). In order to minimise manipulation, we did not capture or measure all breeding pairs. We gathered information on body morphometrics of 70 breeding females ($n = 51, 9$ and 10 at CEL, CON and MOL respectively). We calculated a body size index (BSI hereafter) for reducing body morphometrics to a unique variable (e.g. Forero et al., 2002b; Genovart et al., 2003a). We used principal component analysis (PCA in SPSS 12.0) of the three morphometrics, particularly the first axis (PC1) since it can summarise most of the variability of those body measurements (Legendre and Legendre, 1998), to combine linear body measurements of breeding females. The BSI was defined as the first principal component of the three morphometrics, accounting for 51% of the total variation. Additionally, we drew ~1 mL of blood which was preserved in 70% ethanol and further used for both molecular sexing and stable isotope analysis (see Genovart et al., 2003b and Forero et al., 2002a respectively, for methodological details in sample processing). Individuals

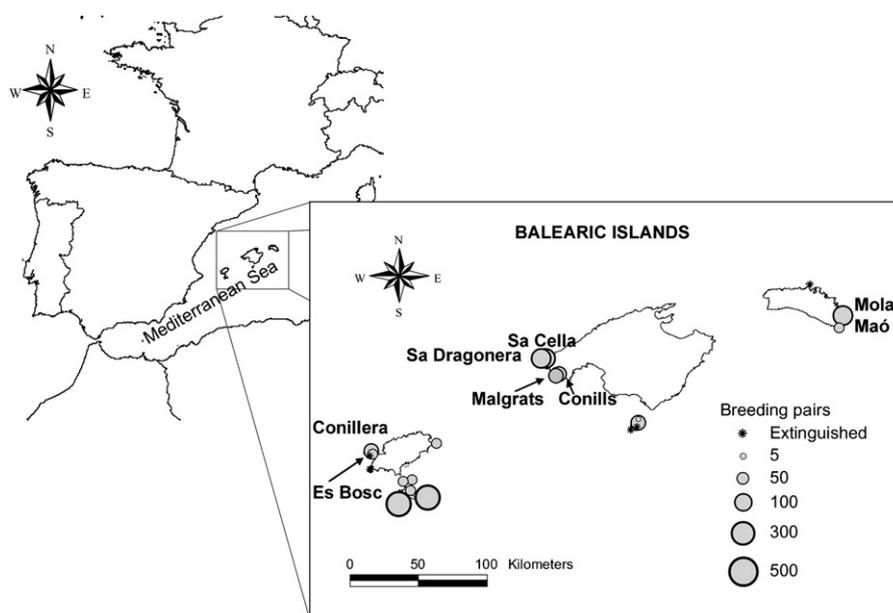


Fig. 1 – Study area and location of the local breeding populations of the Balearic shearwater. Cited local populations in the text are marked.

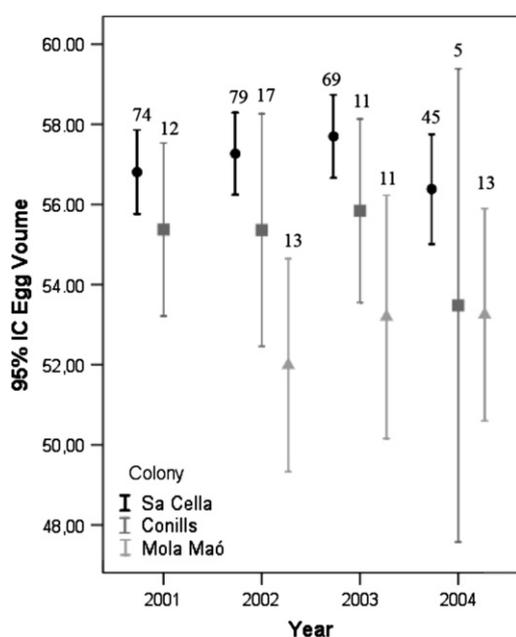


Fig. 2 – Mean egg volume and 95% confidence interval of the surveyed three local populations during the study period (2001–2004). MOL was not sampled in 2001. Sample sizes are shown.

were sexed either using molecular techniques or applying a morphometric discriminant function developed by Genovart et al. (2003a).

2.3. Feeding ecology: stable isotope analyses

We used stable isotope analyses of nitrogen (¹⁵N/¹⁴N, expressed as δ¹⁵N) and carbon (¹³C/¹²C, δ¹³C) for comparing the feeding ecology of Balearic shearwaters at the local population level. Our aim was to assess whether feeding ecology varied similarly with egg size. In seabirds, stable isotopes are a highly valuable tool to discriminate between potential food resources, as indicated by differential trophic levels, and feeding habits (Forero and Hobson, 2003). Values of δ¹⁵N can indicate the trophic level at which adults are feeding, whereas δ¹³C values can indicate feeding habits related to both benthic- vs. pelagic-based food-webs (i.e. fishery discards and small pelagic prey, respectively). For seabirds of the size of the Balearic shearwater, stable isotope values of whole blood

integrate diet information over a period of at least 4 weeks (Hobson and Clark, 1992). Because stable isotopes values can vary depending on the period of the breeding cycle (cf. Schmutz and Hobson, 1998), we randomly took 47 blood samples of both sexes (n = 23, 9 and 15 at CEL, CON and MOL, respectively) from adult breeders during late incubation and early hatching in 2003, representing the diet of shearwaters during the peak incubation period (from mid March to mid April). It is important to note that no trophic segregation have been found between sexes for the Balearic shearwater (Louzao et al, unpublished data).

Ethanol was removed from blood samples prior to stable isotope analysis by decanting and then successive rinsing in distilled water followed by freeze-drying. Stable isotope assays were performed on 1 mg sub-samples of homogenised materials by loading into tin cups and combusting at 1200 °C in a Robo-Prep elemental analyzer the released CO₂ and N₂ were analysed using a continuous-flow isotope ratio mass spectrometer (CFIRMS) with every five unknowns separated by two laboratory standards (albumen). The isotopic composition of the samples was expressed using δ-notation or deviation from international standards in parts per thousand (‰) using the formula: δX = [(R_{sample} - R_{standard})/R_{standard}] × 1000 where X is ¹³C or ¹⁵N and R is the proportion ¹³C/¹²C or ¹⁵N/¹⁴N. The reference standard for ¹³C was the PeeDee Belemnite (PDB) limestone and for ¹⁵N atmospheric N₂. The within-run analytical precision of the procedure was estimated at ±0.1 and ±0.3‰ for stable-carbon and nitrogen-isotope analyses, respectively.

2.4. Statistical analysis

We used generalised linear mixed models (GLMM MIXED procedure, in SAS Institute, 2000) to assess spatio-temporal variability in egg size among local populations, and also the effect of egg size on breeding performance. We assumed that those eggs found in the same nest belonged to the same female due to the high breeding philopatry of Procellariiformes (i.e., low probability of change of breeding pairs between nests) (Warham, 1990). Thus, mixed effects models with the female identity (or nest identity, see below) nested within local population were included as random error terms for accounting for the non-independence of eggs belonging to the same female. Also, local population, year, and both female and nest identity were treated as categorical variables and egg size, BSI, and stable isotopes as continuous variables. We assembled the best-fit model iteratively using a backwards stepwise procedure starting from a saturated model, and rejecting the variables with the lowest explanatory power one at a time (variables were retained when α < 0.05). Contrast analyses were performed when appropriate. Only significant variables are shown for the sake of clarity.

We first performed a preliminary analysis to test if egg volume (denoted by v) could depend, at least partially, on maternal body size. For this analysis, we gathered information on 48, 8 and 10 breeding females of CEL, CON, and MOL, respectively, from which 27, 4 and 2 breeding females presented repeated measurements across years. In the case of CEL, eggs of 14 females were measured twice, 10 three times and 3 four times, whereas in CON, eggs of 1 female were

Table 1 – Morphological measurements (mean ± SD in mm) of 70 breeding females of Balearic shearwater used to calculate a body size index (BSI). Sample sizes are shown in parentheses

Morphological measurement	Local population		
	CEL (n = 51)	CON (n = 9)	MOL (n = 10)
Head plus bill length	86.82 ± 2.31	87.12 ± 2.08	84.69 ± 2.80
Bill depth at nostrils	8.96 ± 0.44	9.04 ± 0.37	8.32 ± 0.35
Tarsus	49.47 ± 1.44	49.04 ± 1.22	46.54 ± 1.71

measured twice, 1 three times and 1 four times and in MOL, eggs of 2 females were measured twice. The saturated model was designed with local population (denoted by c), female BSI, and their interaction as fixed effects ($v = \text{BSI} + c + \text{BSI} * c$), and we fitted year and female identity (instead of nest identity in order to consider female effects) nested within local population as random terms, following a normal distribution using an identity-link function. No significant effect of maternal body size on egg size was found (see Section 3), so further analyses did not include this factor as explanatory variable. After this preliminary analysis, we assessed the spatio-temporal variability in egg size and the saturated model was designed with local population, year (denoted by t), and their interaction as fixed effects ($v = c + t + c * t$), and nest identity (nested within local population) as random effect, following a normal distribution using an identity-link function.

Similarly, for breeding performance (both hatching and breeding success), the saturated model was designed as the additive model of egg size, local population and year (breeding performance = $v + c + t$), and nest identity (nested within local population) as random effects. Hatching and breeding success were treated as binomial dependent variables and fitted using a logit-link function. No interaction terms were introduced as fixed effects due to the small sample size.

When analysing inter-population differences on maternal body size and feeding ecology ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) we only tested local population effect, therefore generalised linear models (GLMs GENMOD procedure, in SAS Institute, 2000) were used instead. Maternal body size and stable isotope data were fitted following a normal distribution using an identity-link function.

3. Results

3.1. Spatio-temporal patterns of egg size and its influence on breeding performance

In relation to egg size and female body size relationship, we collected information on BSI of 66 breeding females associated with 118 egg measurements ($n = 48, 8$ and 10 at CEL, CON and MOL, respectively). From the saturated model ($v = \text{BSI} + c + \text{BSI} * c$), the backward procedure selected the local population effect ($F_{2,63} = 6.31, P = 0.003$) as significant. Therefore, since we did not find any significant relationship between egg size and female BSI in a sub-sample of 118 eggs, we were able to recover the information gathered on the total of 349 eggs to analyse its spatio-temporal variability. Again, from the saturated model ($v = c + t + c * t$) the local population effect was significant ($F_{2,181} = 13.38, P < 0.001$). Contrast analyses showed that differences between CEL vs. MOL and CON vs. MOL were significant ($F_{1,181} = 26.0, P < 0.001$ and $F_{1,181} = 6.97, P = 0.01$), whereas differences between CEL vs. CON were not ($F_{1,181} = 2.60, P = 0.109$) (Fig. 2).

For both hatching and breeding success (saturated model: breeding performance = $v + c + t$) the final model found only the year effect as significant for both breeding parameters (hatching success $F_{3,123} = 3.42, P = 0.020$; breeding success $F_{3,121} = 3.01, P = 0.033$) in CEL and CON.

3.2. Inter-population comparison of maternal body size and feeding ecology

Regarding maternal body size comparison at the population level, we found a significant local population effect in BSI ($\chi^2_2 = 26.42, P < 0.001$). Contrast analyses showed that only differences between CEL vs. MOL ($\chi^2_1 = 26.39, P < 0.001$), and CON vs. MOL ($\chi^2_1 = 12.62, P < 0.001$) were significant. Females from MOL were smaller than those from CEL and CON (Fig. 3).

We found a significant local population effect in $\delta^{15}\text{N}$ values ($\chi^2_2 = 31.51, P < 0.001$), but not in $\delta^{13}\text{C}$ values ($\chi^2_2 = 0.57, P = 0.753$). Values of mean $\delta^{15}\text{N}$ ranged from $9.3 \pm 0.7\text{‰}$ in MOL to $10.4 \pm 0.3\text{‰}$ in CEL, CON presenting intermediate values. All possible contrast analyses of $\delta^{15}\text{N}$ were significant (CEL vs. CON ($\chi^2_1 = 5.22, P = 0.022$); CEL vs. MOL ($\chi^2_1 = 31.51, P < 0.001$), and CON vs. MOL ($\chi^2_1 = 8.65, P = 0.003$)) indicating possible trophic segregation (i.e. foraging at different trophic level) between local populations, with individuals from MOL foraging at lower trophic levels than in CEL and CON. On the other hand, mean $\delta^{13}\text{C}$ values ranged from $-19.4 \pm 0.3\text{‰}$ in CON to $-19.3 \pm 0.2\text{‰}$ in MOL (see Fig. 4), suggesting similar feeding habits among populations.

4. Discussion

4.1. Spatial patterns of egg size variability

Our results showed egg size differences among neighbouring local populations, even though we did not expect variations at such a small spatial scale due to their similar ecological features (e.g. breeding habitat, oceanographic conditions). The variability found in our study could partly be explained

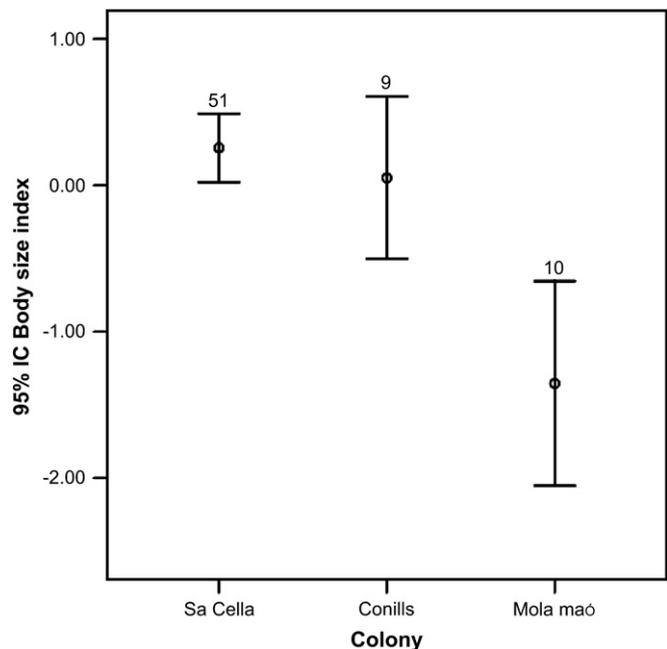


Fig. 3 – Body size index of 70 breeding females of the Balearic shearwater in the three local populations during 2001–2004. Sample sizes are shown.

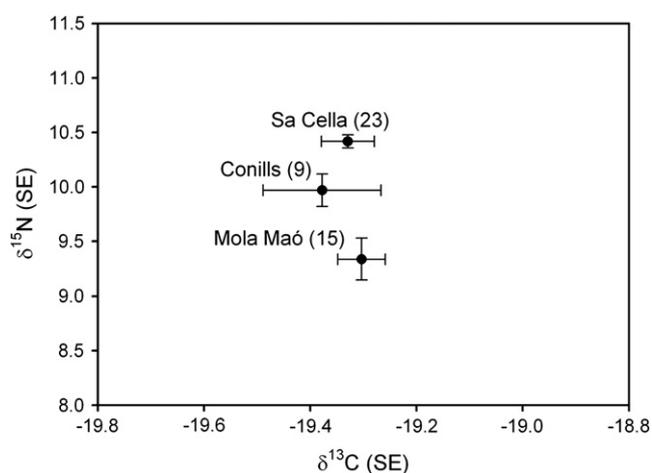


Fig. 4 – Mean (\pm SE) stable-carbon and nitrogen-isotope ratios in blood samples of adults representing the diet of Balearic shearwaters during the peak incubation period (from mid March to mid April) in the three studied local populations in 2003. Sample sizes are shown.

by unexpected differences in feeding ecology among local populations: mean $\delta^{15}\text{N}$ values revealed inter-population variability in trophic level (maximum differences $\sim 1\%$, or a third of a trophic level). At the same time, trophic level varied similarly among local populations showing a similar general pattern compared to egg size, suggesting a nutritional link between them at the population level (larger egg size potentially related to higher $\delta^{15}\text{N}$ mean values). Thus, egg size could be affected by differences in feeding resources and/or behavioural plasticity. In the other hand, $\delta^{13}\text{C}$ values suggested that breeders from different local populations did not differ in general feeding habits (similar mean $\delta^{13}\text{C}$ values) and both benthic and pelagic-based food-webs (i.e. fishery discards and small pelagic prey, respectively) have proved to be important foraging resources for the species (see Arcos and Oro, 2002; Louzao et al., 2006a). However, our interpretations from the stable isotopes need to be taken with caution since we did not investigate in detail the isotopic nature of the food-webs used by each of the local populations. Thus, the baseline $\delta^{15}\text{N}$ values may differ causing different $\delta^{15}\text{N}$ values for food items at the same trophic level (e.g., Schell et al., 1998). However, this seemed unlikely due to the proximity of the local populations (CEL and CON separated ~ 15 km and Mallorca and Menorca ~ 160 km), and to the fact that we only observed differences in $\delta^{15}\text{N}$ values and not in $\delta^{13}\text{C}$ values among local populations. Other Procellariiformes species have shown differences in feeding ecology among populations (Montevecchi et al., 1992 and references therein; Forero et al., 2005), but always at larger spatial scales than that of our study, attributed to contrasting local environmental conditions affecting each local population (see also Frederiksen et al., 2005).

Both trophic level and egg size could probably be influenced by parental body size at the local population level, a potential indicator of a genetic component, since it could probably mediate prey selection (i.e. larger body sizes foraging upon higher trophic levels) (cf. Barbraud et al., 1999; Forero et al., 2002b). Differences in egg size between Mallorca and

Menorca would be, at least partially, explained by differences in body size, since at the latter local population there is evidence of a genetic introgression of its smaller sibling species, the Yelkouan shearwater *P. yelkouan*, and this drives body size differences between individuals from both islands (Genovart et al., 2007). The most likely event for explaining this introgression is an historical secondary contact between the two species in Menorca (the closest colony to the range of the Yelkouan shearwater) (Genovart et al., 2007). Similarly, Amundsen (1995) and Mougin (1998) found differences in egg size due to local genetic differences in different subspecies of Snow petrels *Pagodroma nivea* and Cory's shearwater *Calonectris diomedea* respectively, with larger individuals laying bigger eggs. Likewise, demographic analyses have suggested that both local populations from Mallorca do not differ in adult survival, but they could diverge in demographic factors such as age structure (Oro et al., 2004; Tavecchia et al., 2008) (cf. Martin, 1987). However, these demographic differences between local populations from Mallorca have to be taken with caution due to small sample size of CON.

4.2. Temporal variability in egg size and its effect on breeding performance

We found no significant variation in egg size among years, in agreement with data available for single-egg systems (i.e., Procellariiformes: Brooke, 1990; Mougin, 1998; Sagar et al., 2005; but see Croxall et al., 1992; Weidinger, 1996; Michel et al., 2003). Nevertheless, temporal variability affected the breeding performance of Balearic shearwaters, presumably related to temporal stochasticity of prey density (see also Louzao et al., 2006a). Egg size could be a more conservative trait regarding food availability than breeding performance, probably due to the differential temporal window affecting both breeding parameters: egg formation represents a short-term energetic investment compared to the long-term period affecting breeding performance (see Ricklefs, 1990).

The absence of any relationship between egg size and breeding performance found in our study also agrees with other studies on Procellariiformes suggesting that egg size may not influence on this fitness-related factor (Meathrel et al., 1993; Weidinger, 1996; Mougin, 1998; but see Croxall, 1992). Christians (2002) suggested that larger eggs might only confer an advantage in harsh, low-quality conditions, when females invest part of their energetic reserves laying an egg of sufficient quality (i.e. minimum or similar egg size) to produce offspring of high quality (Ricklefs, 1990; Weimerkirch et al., 2001). Alternatively, different authors have pointed out the importance of parental quality rather than egg size in offspring survival (Saether et al., 1997). However, factors related to maternal characteristics (i.e. female age, mass and size), and foraging skills (e.g., food availability and quality) are difficult to disentangle since they are not independent (Christians, 2000).

In summary, inter-population differences in both body size and environmental factors could influence egg size variability at the population level in the Balearic shearwater at small spatial scales. Moreover, the parallel trend between egg size and assumed trophic level suggests a nutritional link between them at the population level. Further research is needed to

explore the variability of trait values in animals, bridging the gaps between body size and environmental determinants at different spatio-temporal scales.

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