

RESEARCH ARTICLE

It's not all abundance: Detectability and accessibility of food also explain breeding investment in long-lived marine animals

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Abstract

Large-scale climatic indices are extensively used as predictors of ecological processes, but the mechanisms and the spatio-temporal scales at which climatic indices influence these processes are often speculative. Here, we use long-term data to evaluate how a measure of individual breeding investment (the egg volume) of three long-lived and long-distance-migrating seabirds is influenced by i) a large-scale climatic index (the North Atlantic Oscillation) and ii) local-scale variables (food abundance, foraging conditions, and competition). Winter values of the North Atlantic Oscillation did not correlate with local-scale variables measured in spring, but surprisingly, both had a high predictive power of the temporal variability of the egg volume in the three study species, even though they have different life-history strategies. The importance of the winter North Atlantic Oscillation suggests *carry-over* effects of winter conditions on subsequent breeding investment. Interestingly, the most important local-scale variables measured in spring were associated with food detectability (foraging conditions) and the factors influencing its accessibility (foraging conditions and competition by density-dependence). Large-scale climatic indices may work better as predictors of foraging conditions when organisms perform long distance migrations, while local-scale variables are more appropriate when foraging areas are more restricted (e.g. during the breeding season). Contrary to what is commonly assumed, food abundance does not directly translate into food intake and its detectability and accessibility should be considered in the study of food-related ecological processes.

Introduction

An important challenge in the study of population fluctuations is to reveal the link between demographic parameters and climatic variables, mediated by their influence on foraging resources [1–3]. It is difficult, however, to single out the effect of a single climatic variable on a

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given biological system because variables can act directly [4], indirectly through multiple paths [5], alone [6] or in combination with others [7]. For this reason, large-scale climatic indices are often preferred as predictors of ecological processes than local variables, because they integrate environmental changes over different temporal and spatial scales [8–11].

The North Atlantic Oscillation (NAO) and the Southern Oscillation indices (SOI), for example, have been used in many studies as ecological predictors in both terrestrial and marine ecosystems (see [12, 13] and references therein). In marine ecosystems, the winter NAO (hereafter wNAO) is known to influence demographic parameters, such as reproductive success and survival in long-lived and long-ranging top predators [14–16]. It is often assumed that the influence of these large-scale climatic indices occurs *via* their influence on local climatic variables (see [12, 17] and references therein) and/or *via* the indirect effects on local food abundance (see [9, 12, 18] and references therein). However, in many cases, the mechanisms and the spatio-temporal scales through which these climatic indices influence demographic parameters remain largely unexplained or speculative [8, 19].

The combined use of large-scale climatic indices and local-scale variables should reveal their relative role and describe the mechanisms and the spatio-temporal scale at which they influence these demographic parameters [20–23]. The Scopoli's shearwater *Calonectris diomedea*, the Sandwich tern *Thalasseus sandvicensis*, and the Audouin's gull *Ichthyaeetus audouinii* are three examples of long-lived and long-distance migratory marine top predators. These three species breed sympatrically in the western Mediterranean, have different life-histories and feed at different depths in the water column: gulls are surface feeders, terns make short diving plunges and shearwaters perform much deeper and longer foraging dives. Furthermore, terns and gulls can modulate clutch size depending on environmental conditions, whereas shearwaters lay a single egg. Despite these differences, foraging areas of the three species overlap both during the breeding [24–26] and wintering seasons [27, 28], in particular along the western coasts of Africa (Figs 1 and 2). Like most avian species, these seabirds can regulate breeding investment by adjusting egg number (terns and gulls) and size [29]. Egg volume in birds has an important genetic component [30], but in long-lived birds, its temporal variance constitutes a reliable indicator of environmental conditions (e.g. food availability) and individual breeding investment [31–33]. Moreover, egg volume can be correlated with chick growth and survival [34–37].

Using long-term monitoring data of Scopoli's shearwater, Sandwich tern, and Audouin's gull populations, we assess the influence of i) winter and spring values of the North Atlantic Oscillation index and ii) local-scale food-related variables measured in spring (during breeding) as predictors of the average egg volume in a clutch. For these local-scale variables, we included the factors potentially influencing food detectability and accessibility (foraging conditions and both intraspecific and interspecific competition) and per capita food abundance. Given the smaller area used by seabirds during the breeding period relative to the winter distribution, we expect local variables to be a better predictor than the North Atlantic Oscillation index on egg volume.

Methods

Field data and study area

Sandwich tern and Audouin's gull eggs were measured at the Ebro Delta while eggs of Scopoli's shearwaters were measured about 170km east, at Dragonera Island (Balearic archipelago; Fig 1). Previous studies based on observations and direct tracking of marked individuals indicate that adults of the three species forage actively within the Ebro Delta continental shelf [27, 28]; thus, we considered the continental shelf of a marine area of 100km radius centred on the

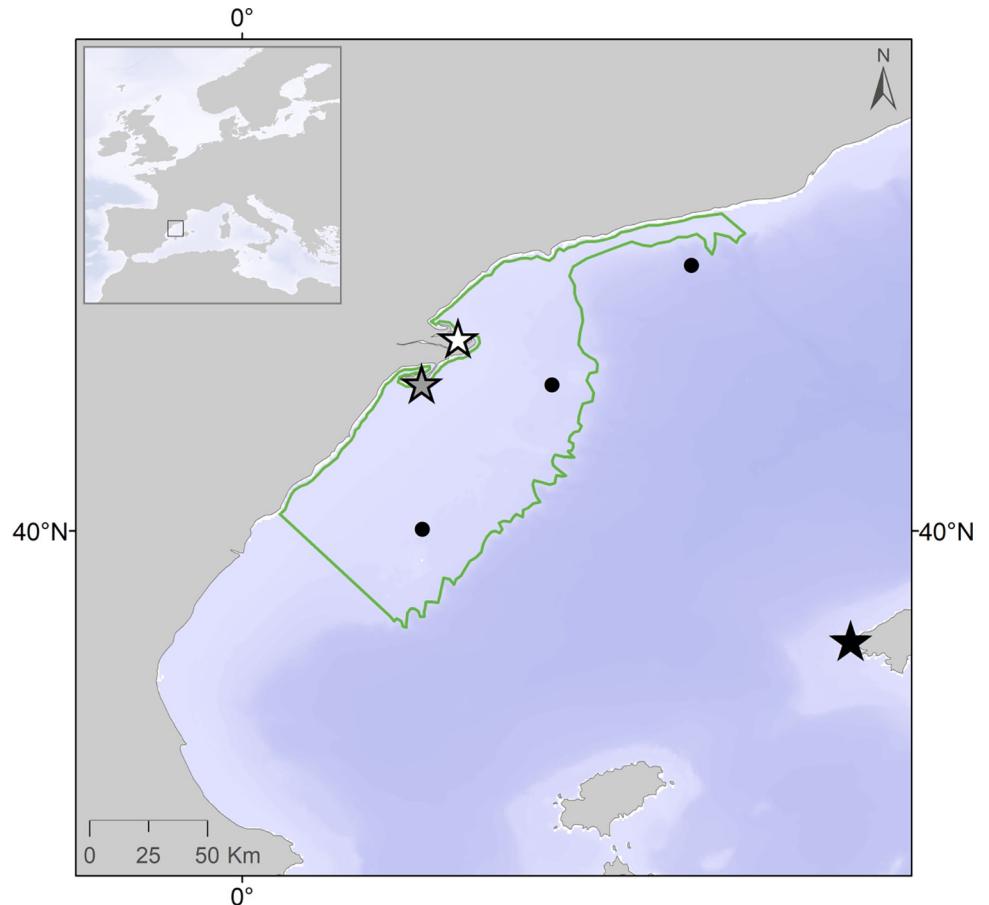


Fig 1. Common foraging area (delimited by the green line) of studied populations during the breeding season within the Ebro Delta continental shelf (Western Mediterranean) and locations of breeding colonies of studied populations of the Scopoli's shearwater (black star), the Sandwich tern (grey star) and the Audouin's gull (white star). Black dots represent stations where local climatic and oceanographic variables (wind speed and direction, wave height, and seawater turbidity) were measured to assess foraging conditions for studied populations during the early breeding season.

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Ebro Delta as representative of their common foraging area (Fig 1). The three species mostly winter off the Atlantic coasts of Africa [27, 28], but gulls are partial migrants and part of their population remains along the Western Mediterranean coast [27]. For each species, we recorded the temporal variance of the annual mean volume of the modal clutch (hereafter, egg volume; $N = 10573$ clutches in total) as an indicator of the metabolic resources accumulated for breeding [31, 32]. Long-term data were collected for Scopoli's shearwaters (1440 one-egg clutches measured from 2001 to 2017), Sandwich terns (425 two-egg modal clutches measured between 2000 and 2016), and Audouin's gull (8708 three-egg modal clutches measured between 2001 and 2017). Eggs were measured with a digital caliper to $\pm 0.01\text{mm}$ and egg volume (V) was calculated in cm^3 according to the equation $V = K \times L \times W^2$ [38], where L = maximum egg length and W = maximum egg width and K is a species-specific egg-shape constant: 0.510×10^{-3} for shearwaters and terns and 0.467×10^{-3} for gulls. Once measured, all the eggs were returned to the nest, therefore, Institutional Animal Care and Use Committee (IACUC) was not required. Despite being an important predictor of across individuals variation in egg volume [30], female size was not available for all nests and was assumed to be a random and additive component of the total variance within each colony [39]. The Governments

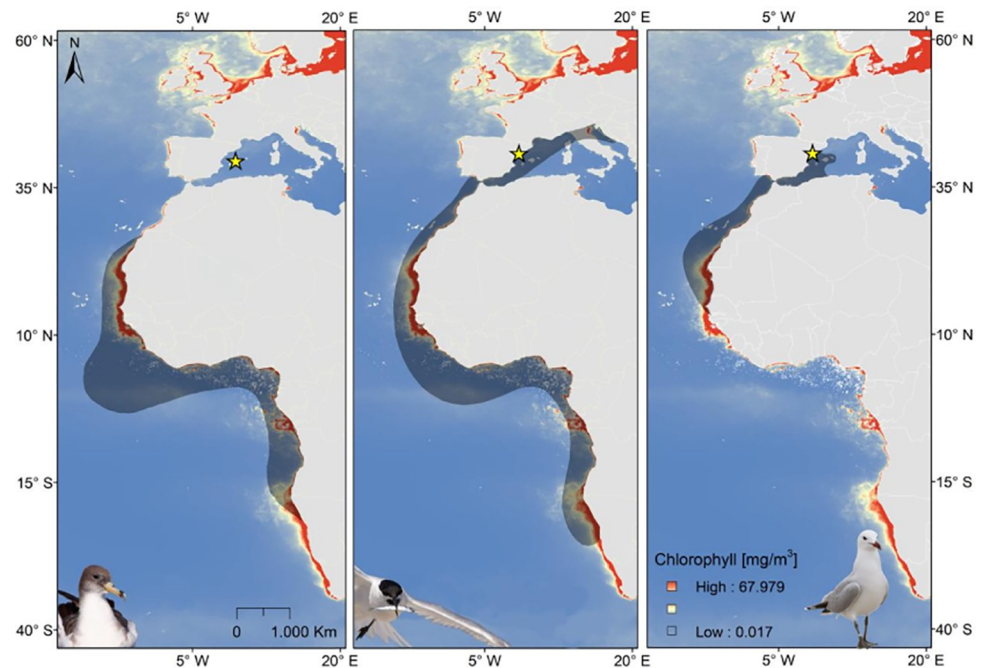


Fig 2. Wintering areas (shaded areas) of studied populations of the Scopoli's shearwater (left; data from Reyes-González et al 2017), the Sandwich tern (center; data from Institut Català d'Ornitologia), and the Audouin's gull (right; data from Bécères et al 2015). Yellow stars indicate the location of the breeding colonies where eggs were measured. Mean annual sea surface concentration of chlorophyll-a for the period 2009–2013 is also shown (data obtained at <http://data.unep-wcmc.org/datasets/37>).

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of the Balearic Islands (Servei de Protecció d'Espècies of the Conselleria de Medi Ambient of the Balearic Government) and Catalonia (Generalitat de Catalunya) provided the permits to work with each species studied. Access permits to protected areas were provided by Sa Dragonera Natural Park (Consell de Mallorca) and the Ebro Delta Natural Park respectively. The field studies did not involve endangered or protected species. All sampling procedures and/or experimental manipulations were reviewed and approved by the corresponding authorities after obtaining the field permit.

Predictors of egg volume

The large-scale climatic index. We used winter means (December to March) of the station-based North Atlantic Oscillation index (wNAO) (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>) to assess the relative importance that winter conditions in the year i (December $i-1$ to March i) has on predicting the egg volume of the following breeding season. Spring means (considering the species-specific early breeding season; see [S4 Table](#)) of the North Atlantic Oscillation (spNAO) were also used to assess the possible influence exerted by this climate index during spring months when the study species were laying eggs.

Seawater turbidity, wave height, and wind speed and direction. We assume that in the foraging process, animals first detect food and then try to access it. For this reason, we use the term 'accessibility' to refer to those physical barriers that hinder access to food once detected. To assess how local climatic and oceanographic variables influence the annual variance of the egg volume of the studied species we used monthly means of i) wind speed and direction, ii) wave height and iii) seawater turbidity as proxies of detectability and accessibility of food, [40,

41]. Data on wind speed ($\text{m}\cdot\text{s}^{-1}$), wind direction (degrees), and wave height (m) based on numeric modelling data were obtained from the SIMAR dataset at <http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx>. To account for a cumulative effect on foraging conditions, the number of days of winds blowing from each quartile (Q1: 0° - 90° ; Q2: 91° - 180° ; Q3: 181° - 270° and Q4: 271° - 360°) were multiplied by the corresponding mean wind speed ($\text{day}\cdot\text{m}\cdot\text{s}^{-1}$). Finally, seawater turbidity was estimated by considering the diffuse attenuation coefficient of light at 490 nm (kd_{490}) (1 Km^2 resolution) from multi-satellite observations (<http://marine.copernicus.eu/services-portfolio/access-to-products/>).

Intra- and inter-specific competition during the early breeding season. To assess the potential effect that intra-specific competition has on the temporal variance of the egg volume we used annual estimates of breeding pair numbers for each studied species. Population estimates of gulls and terns were obtained by direct counts. For Audouin's gull, estimates were based on annual censuses from three different colonies as these birds are known to share the same foraging area during the breeding season (Ebro Delta, Castellón, and Tarragona). For the Scopoli's shearwater, population size was estimated using the number of nests occupied in the study colony each year [42]. The effect of interspecific competition for food was assessed by considering the total number of breeding pairs of the three seabird species (S5 Table) as well as of the Yellow-legged gull *Larus michahellis*, an abundant generalist species competing for the same foraging resources (i.e. sardines, anchovies and trawling fishery discards) in the study area.

Per capita food abundance during the early breeding season. As a measure of natural and anthropogenic food resources, we used annual estimates of the *per capita* abundance of natural prey and fishery discards during the early period of the species-specific breeding season (S4 Table). Temporal variability in the abundance of natural prey was approximated by using the catch per unit effort (hereafter 'CPUE') of sardines *Sardina pilchardus* and anchovies *Engraulis encrasicolus*, the most abundant small pelagic species in the study area [43, 44] and prey of the three studied species [45–48]. CPUE was obtained by dividing the total landings (in Kg) of each species by the number of vessels of the main purse seine fleets in the area (S4 Table). Data on landings and number of fishing vessels were facilitated by the Direcció General de Pesca i Afers Marítims of the Generalitat de Catalunya. We used the sum of the main horsepower declared by trawl fleets in the study area (S4 Table) as a proxy of the abundance of fishery discards [33]. Trawl horsepower is a more precise estimate of discards generated than the number of vessels because the more horsepower the bigger are the nets used. Data on trawl horsepower were obtained from the European Commission Fleet Register at <http://ec.europa.eu/fisheries/fleet/index.cfm>. *Per capita* abundance of natural prey and fishery discards was calculated by dividing estimates of each resource type by the total number of breeding pairs of the main seabird species competing for each specific resource (S5 Table).

Data analysis

We analyzed factors affecting the egg volume and their statistical interactions using generalized linear models in software R (R Development team 2014), with mean egg volume of the modal clutch (the most repeated clutch size among observations) as dependent variable. Covariates were centered and scaled to equalize their means and obtained comparable standard deviations. A diagnosis was made to check assumptions of the models (linearity normality, homogeneity of variance and independence of residuals). We began the analysis by calculating the correlation coefficient across all covariates described above to avoid the simultaneous presence of highly correlated covariates (collinearity) and only uncorrelated covariates (p value >0.05) were considered together in the models. For the best models, we also run tests

to check the variance inflation factors (VIFs). Only models where all VIF values were <3 were considered [49]. To check VIFs in models with interaction terms we first centered these covariates as suggested by [50]. All covariates were taken as fixed effects. Only model structures that made ecological sense according to species-specific diet and foraging strategies were compared. Information theory based on Akaike Information Criterion (AIC; [51, 52]) was used to select the best explanatory models. Best models were those with the lowest AIC and models with AIC differences ≤ 2 were considered equivalent [52]. The proportion of total annual variance in egg volume explained by covariates was calculated as $[\text{deviance}(\text{model constant}) - \text{deviance}(\text{model with covariate})] / [\text{deviance}(\text{model constant}) - \text{deviance}(\text{model time-dependent})]$. The resulting statistics can be used as an equivalent of the coefficient of determination, R^2 (hereafter R^2 ; see [53]).

Results

Scopoli's shearwater

For the Scopoli's shearwater, the model with the lowest AIC value included the additive effect of the wNAO and the statistical interaction between the wave height and the *per capita* abundance of fishery discards (Model 1 in Tables 1 and S1 and Fig 3A). According to this model, high values of wave height decreased the egg volume, even when fishery discards per capita were abundant. The wNAO had a negative effect on the egg volume whilst the effect of fishery discards was positive. When assessing wNAO and local conditions separately, the percentage of the total annual variance of the egg volume explained by the wNAO was 45% (Model 5 in Tables 1 and S1), while the model considering only local conditions (Model 3 in Tables 1 and S1) explained 66%. When tested simultaneously (wNAO, wave height, and fishery discards), these covariates explained 79% of the total annual variance of the egg volume (Model 1 in Table 1 and S1; Fig 3A). S1 Fig shows the relationship between the egg volume predicted by Model 1 and the egg volume observed. We did not find a significant effect of the number of potential competitors (Tables 1 and S1) nor of the spNAO.

Table 1. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Scopoli's shearwater based on Akaike information criterion values (AIC) and Akaike weights (Wi).

Model	Notation	Deviance	df	AIC	Δ AIC	Wi
1	Winter NAO + WaveHeight * DiscardsPC	40733.54	6	8911.61	0.00	0.85
2	Winter NAO + WaveHeight + DiscardsPC	40899.95	5	8915.48	3.87	0.12
3	WaveHeight * DiscardsPC	40966.80	5	8917.83	6.22	0.04
4	Winter NAO + WaveHeight	41035.65	4	8918.25	6.88	0.03
5	Winter NAO	41331.38	3	8926.59	14.98	0.00
6	WaveHeight	41478.83	3	8931.72	20.11	0.00
7	Compet. by AG	41558.13	3	8934.47	22.86	0.00
8	Wind4Q	41602.25	3	8936.00	24.39	0.00
9	Discards PC	41635.50	3	8937.15	25.54	0.00
10	Wind3Q	41693.72	3	8939.16	27.55	0.00

The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, SS = Scopoli's shearwater, YLG = Yellow-legged Gull, AG = Audouin's Gull, PC = per capita, Wind1Q, 2Q, 3Q, and 4Q = 1st, 2nd, 3rd and 4th quartile winds respectively (see methods section), Discards = fishery discards, Null model is an only-intercept model. Discards PC and Sardine PC consider the number of individuals of YLG+AG+SS.

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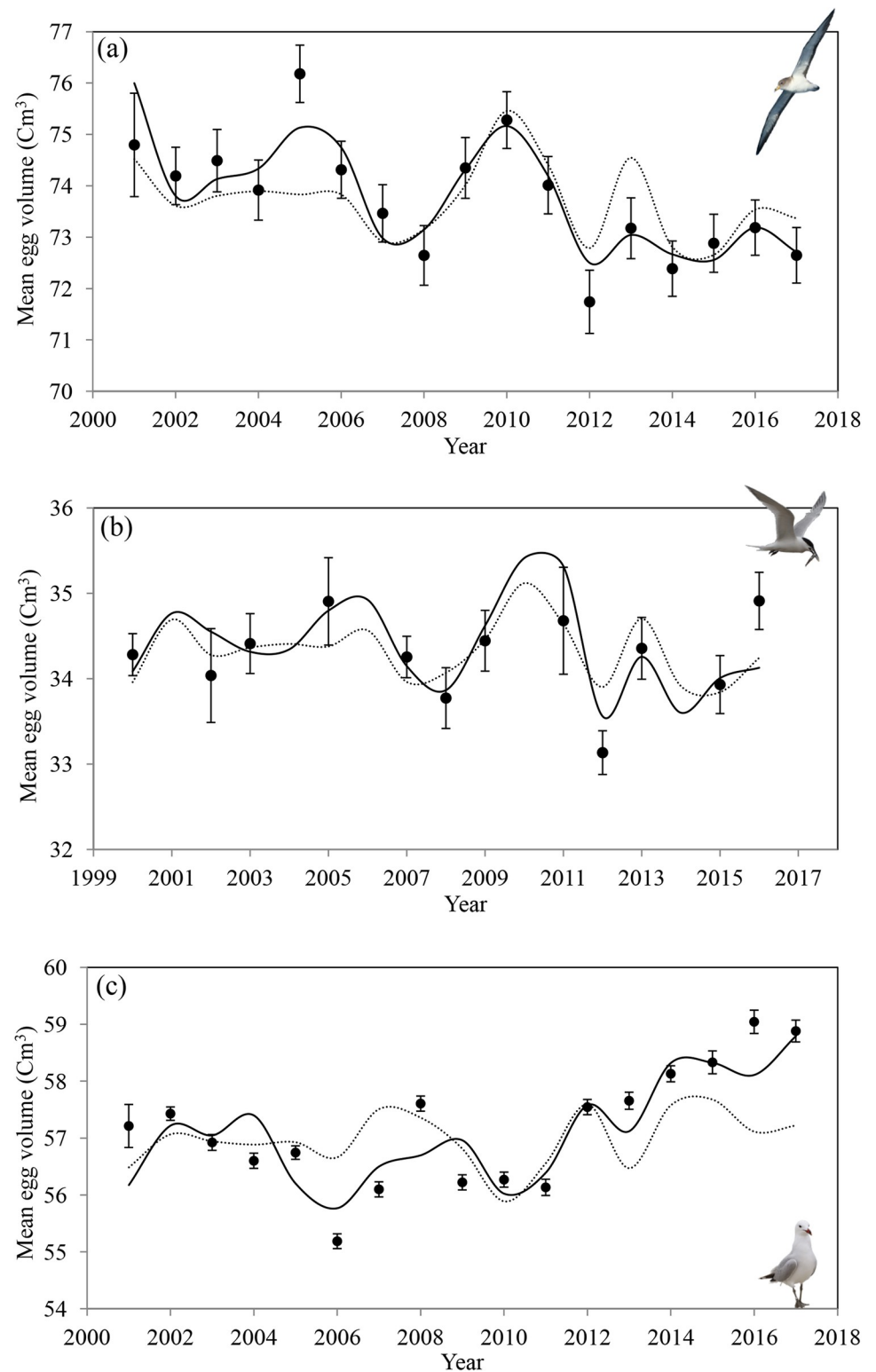


Fig 3. Time series with the observed mean egg volume \pm standard error (black circles) and the expected mean egg volume according to best explanatory models (black line) in (a) the Scopoli's shearwater (Model 1, Tables 1 and S1), (b) the Sandwich tern (Model 1, Tables 2 and S2) and (c) the Audouin's gull (Model 1, Tables 3 and S3). Models only considering winter conditions (wNAO) are also shown (dotted line).

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Table 2. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Sandwich tern based on Akaike information criterion values (AIC) and Akaike weights (Wi).

Model	Notation	Deviance	df	AIC	Δ AIC	Wi
1	Winter NAO + Wind3Q + Turbidity	1655.94	5	1787.71	0	0.23
2	Winter NAO + Wind3Q	1665.30	4	1788.10	0.39	0.19
3	Winter NAO + Wind3Q + Turbidity + Compet. by YLG	1650.57	6	1788.34	0.63	0.17
4	Winter NAO + Wind3Q + Compet. by YLG	1662.09	5	1789.28	1.57	0.10
5	Winter NAO + Wind3Q + AnchovyPC	1659.32	5	1789.58	1.87	0.08
6	Winter NAO + Wind3Q * Turbidity	1655.69	6	1789.65	1.94	0.09
7	Winter NAO + Wind3Q + Wind1Q	1664.41	5	1789.87	2.16	0.08
8	Winter NAO	1689.33	3	1792.16	4.45	0.02
9	Wind3Q	1690.22	3	1792.38	4.67	0.02
10	Wind3Q + Turbidity	1689.84	4	1794.30	6.59	0.01

The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, YLG = Yellow-legged Gull, PC = Per capita, Wind1Q, 2Q, 3Q, and 4Q = 1st, 2nd, 3rd and 4th quartile winds respectively (see [methods](#) section), Discards = fishery discards, Null model is an only-intercept model. Both, discards PC and anchovy PC consider the number of individuals of ST, YLG, AG, and SS.

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Sandwich tern

For the Sandwich tern, the best model suggested that egg volume was associated with the additive effect of the wNAO and food detectability and accessibility in the form of 3rd quartile winds and seawater turbidity (Model 1 in Tables 2 and S2 and Fig 3B). For all three covariates, positive values had a negative effect on the egg volume. Assessed alone, the wNAO explained 28% of the total annual variance (Model 8 in Tables 2 and S2), while local conditions explained 27% (Model 10 in Tables 2 and S2). All three covariates exerted a negative effect on the egg volume. When these covariates were tested simultaneously (Model 1 in Tables 1 and S1; Fig 3A), they explained 59% of the total annual variance. S2 Fig shows the relationship between the egg volume predicted by Model 1 and the egg volume observed. Models 2 to 6 including the additive effect of the interspecific competition exerted by Yellow-legged gulls, seawaters, turbidity, abundance of anchovy or the statistical interaction with the 3rd quartile winds, had similar explanatory power to Model 1 (i.e. Δ AIC values < 2; Tables 2 and S2). However, both the interaction and the additive terms in models 2 and 6 act as pretending variables. Pretending variables occur when after adding a new variable in a model, an Δ AIC~2 is obtained but, the deviance does not decrease [54] and should not be considered further (Appendix B in [55]).

Audouin's gull

Model information theory indicated that Audouin's gull egg volume was influenced by the wNAO and the statistical interaction between the intra-specific and inter-specific competition (Model 1 in Tables 3 and S3 and Fig 3C). The wNAO had a positive effect on egg volume, while the effect of both intra- and inter-specific competition was negative. When tested individually, the percentage of the total annual variance of the egg volume explained by the wNAO was 24% (Model 10 in Tables 1 and S1), while the effect of competition (intra- and inter-specific) explained 59% (Model 4 in Tables 3 and S3). Tested simultaneously (Model 1 in Tables 3 and S3 and Fig 3C), these covariates explained 70% of the annual variance of the egg volume. S3 Fig shows the relationship between the egg volume predicted by Model 1 and the egg volume observed. Population density in this species was correlated with the abundance of natural prey, fishery discards, and inversely correlated with wave height (see S8 Table for more

Table 3. Generalized linear models explaining egg volume variability (mean egg volume in a clutch) of the Audouin's gull based on Akaike information criterion values (AIC) and Akaike weights (Wi).

Model	Notation	Deviance	df	AIC	Δ AIC	W
1	Winter NAO + Intrasp. compet. * Compet. by YLG	94498.10	6	45482.82	0.00	1.00
2	Winter NAO + Intrasp. compet. + Compet. by YLG	94640.28	5	45493.91	11.09	0.00
3	Winter NAO + Intrasp. compet.	94695.19	4	45496.96	14.14	0.00
4	Intraspecific competition * Competition by YLG	95377.26	5	45561.45	78.63	0.00
5	Intraspecific competition	95560.62	3	45574.18	91.36	0.00
6	Sardine PC	95927.54	3	45607.54	124.72	0.00
7	Wave height	97782.89	3	45774.34	291.52	0.00
8	Anchovy PC	97811.19	3	45776.86	294.04	0.00
9	Winter NAO	98076.86	3	45800.48	317.66	0.00
10	4 th q. winds	98114.50	3	45803.82	321.00	0.00

The best explanatory model (Model 1) is the one with the lowest AIC. In the notation: Winter NAO = winter North Atlantic Oscillation, Spring NAO = Spring North Atlantic Oscillation during the species-specific pre-laying period, YLG = Yellow-legged Gull, AG = Audouin's Gull, SS = Scopoli's shearwater, PC = Per capita, Discards = fishery discards, Null model is an only-intercept model. Discards PC, Sardine PC, and Anchovy PC consider the total number of individuals of the three study species.

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details). Therefore, to avoid collinearity these covariates were not considered together in our models. Contrary to the other species considered, the effect of the wNAO on the egg volume of the Audouin's gull was positive.

Discussion

The effects of the wNAO and the local variables measured in spring were different for each study species, likely due to the differences in life histories, foraging strategies, and wintering geographical ranges. However, for all three species, the temporal variation in average egg volume was better explained when both (local variables measured in spring and wNAO) were considered together.

The additive effect of wNAO on breeding investment found here would indicate a *carry-over* effect of winter conditions on subsequent reproductive seasons [56, 57]. This effect was especially important for shearwaters showing the slowest life history strategy of the three study species [58]. This result also suggests that Cory's Shearwaters act as capital breeders, however further research is needed in this regard, so this possibility should be taken with caution. The wNAO and winter anomalies influence wind speed and direction and the wave height in the Atlantic Ocean and the Mediterranean Sea [59]. High values of wNAO likely drove adverse foraging conditions for shearwaters during wintering and a poorer body condition for the subsequent breeding season. The wNAO influenced negatively the egg volume of shearwaters and sandwich terns but had a positive influence on the egg volume of the Audouin's gull. A plausible explanation is that many gulls remain in the Western Mediterranean during winter (see Fig 2; [27, 28]), where positive values of the wNAO are associated with less stormy winters (see e.g. [60]). [8] found that bird species wintering in the Mediterranean area had different responses to the wNAO when compared to species wintering in northern Europe. Another non-exclusive explanation is that intra- and inter-specific competition has greater importance than other effects especially for Audouin's gulls, which are outcompeted by the larger yellow-legged gull for the same size and type of food [61]. Different responses to the wNAO could also be associated with differences in species-specific foraging strategies (e.g. terns and gulls can cope with adverse weather conditions by feeding in sheltered coastal areas, while shearwaters

only feed in the open sea). Finally, these differences could also be related to the fact that the study species have different evolutionary life histories: terns and gulls are multiparous, while shearwaters lay a single egg. Interestingly, local variables related to food detectability and accessibility (oceanographic physical features; see e.g. [40, 41, 62]) and competition during the early breeding season were more important than food abundance. This implies that food abundance *per se* does not necessarily translate into food intake for predators and that the role played by detectability and accessibility of food in ecological processes deserves more consideration [21, 63, 64].

The relative importance of the variables explaining food detectability and accessibility (wave height, wind speed and direction, seawater turbidity, and competition) also changed for each study species, and once again, this is likely due to differences in their foraging strategies. Larger waves may drive natural prey to deeper waters affecting their detectability and accessibility to shearwaters [40]. Wind may act in opposite ways on fishing conditions depending on its intensity [65]. Strong winds may negatively affect terns' flying trajectories when they pounce on their prey during fishing influencing both, detectability and accessibility of food [40, 66], but favourable winds can result in important energy savings by seabirds on displacements (see e.g. [67–69]). Although weak, we also detected a negative effect of water turbidity on the egg volume of Sandwich terns. Previous studies have shown that water turbidity negatively influences prey detectability of Sandwich terns [41] and other seabird species (see e.g. [20, 70]).

A negative effect of intra- and interspecific competition (exerted by the Yellow-legged gull) was retained for the Audouin's gull only. Competition between the two species of gulls has been previously reported in the Western Mediterranean, and we found that as intraspecific competition increases, interspecific competition decreases [61, 71]. The important role of density-dependence for this species is not surprising, considering that the study colony hold up to 73% of the total world population [45, 72]. Inter- and intra-specific competition for food seemed to overcome the influence of climatic and local oceanographic variables (see [73]). However, the effect of density-dependence was not retained for terns and shearwaters, whose densities were likely underestimated by missing birds coming from neighbouring colonies.

Conclusions

Our results provide new insights on the relative influence of large-scale climatic indices vs local variables on egg volume as a proxy of breeding investment. We showed that both large-scale climatic index and local variables are correlated with breeding investment because they operate at different spatio-temporal scales. The wNAO index acts in the form of a *carry-over* effect arising from winter conditions, while local conditions act as proximate causes of food intake. Finally, and in contrast to what is commonly assumed, food abundance does not necessarily translate into individual food intake. Large-scale climate indices present several advantages as indicators of regulating forces of ecosystems [12, 74], especially when animals are widely distributed in space (e.g. across wintering regions), but local variables may be more important and can provide a better explanation of processes affecting conditions for foraging, including food detectability and accessibility. Further research should focus on fine-tuning the mechanisms through which local variables affect food intake, for example by coupling foraging activity with tracking data and sea-state variables.

Supporting information

S1 Table. Models explaining the egg volume variability of the Scopoli's shearwater.
(DOCX)

S2 Table. Models explaining the egg volume variability of Sandwich terns.

(DOCX)

S3 Table. Models explaining the egg volume variability of the Audouin's gull.

(DOCX)

S4 Table. Species-specific early breeding periods of studied populations.

(DOCX)

S5 Table. Foraging interactions and competition for food among the study species.

(DOCX)

S6 Table. Correlation matrix for the Scopoli's shearwater.

(DOCX)

S7 Table. Correlation matrix for Sandwich terns.

(DOCX)

S8 Table. Correlation matrix for the Audouin's gull.

(DOCX)

S9 Table. Annual values of egg volume and covariates for the Scopoli's shearwater.

(DOCX)

S10 Table. Annual values of egg volume and covariates for Sandwich terns.

(DOCX)

S11 Table. Annual values of egg volume and covariates for the Audouin's gull.

(DOCX)

S12 Table. Estimates \pm SE of the best model for the Scopoli's shearwater.

(DOCX)

S13 Table. Estimates \pm SE of the best models for Sandwich terns.

(DOCX)

S14 Table. Estimates \pm SE of the best model for the Audouin's gull.

(DOCX)

S1 Fig. Egg volume predicted v.s. observed for the Scopoli's shearwater.

(DOCX)

S2 Fig. Egg volume predicted v.s. observed for Sandwich terns.

(DOCX)

S3 Fig. Egg volume predicted v.s. observed for the Audouin's gull.

(DOCX)

S1 File. Supporting information references.

(DOCX)

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References

1. Oro D. Grand challenges in population dynamics. *Front Ecol Evol.* 2013; 1:2. <https://doi.org/10.3389/fevo.2013.00002>. Available from: <https://www.frontiersin.org/articles/10.3389/fevo.2013.00002/full>
2. Jenouvrier S., Holland M., Stroeve J., Serreze M., Barbraud C., Weimerskirch H., et al. Projected continent-wide declines of the emperor penguin under climate change. *Nat Clim Chang.* 2014; 4: 715–718. <https://doi.org/10.1038/nclimate2280>
3. Tavecchia G., Tenan S., Pradel R., Igual J.-M., Genovart M. & Oro D. Climate-driven vital rates do not always mean climate-driven population. *Glob Change Biol.* 2016; 22: 3960–3966. <https://doi.org/10.1111/gcb.13330>
4. Barbraud C., Barbraud J.-C. & Barbraud M. Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis.* 1999; 141: 469–479. <https://doi.org/10.1111/j.1474-919X.1999.tb04416.x>
5. Bentz B.J., Regniere J., Fettig C.J., Hansen E.M., Hayes J.L., Hicke J.A., et al. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience.* 2010; 60(8): 602–613. <https://doi.org/10.1525/bio.2010.60.8.6>
6. Fernández-Chacón A., Bertolero A., Amengual A., Tavecchia G., Homar V. & Oro D. Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise. *Glob Change Biol.* 2011; 17: 3075–3088. <https://doi.org/10.1111/j.1365-2486.2011.02469.x>
7. Molinero J.C., Ibanez F., Nival P., Buecher E. & Souissi S. North Atlantic climate and northwestern Mediterranean plankton variability. *Limnol Oceanog.* 2005; 50: 1213–1220. <https://doi.org/10.4319/lo.2005.50.4.1213>
8. Jonzén N., Hedenström A., Hjort C., Lindström Å., Lundberg P. & Andersson A. Climate patterns and the stochastic dynamics of migratory birds. *Oikos.* 2002; 97: 329–336. <https://doi.org/10.1034/j.1600-0706.2002.970303.x>
9. Hallett T.B., Coulson T., Pilkington J.G., Clutton-Brock T.H., Pemberton J.M. & Grenfell B.T. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature.* 2004; 430: 71–75. <https://doi.org/10.1038/nature02708> PMID: 15229599
10. Stenseth N.C. & Mysterud A. Weather packages: finding the right scale and composition of climate in ecology. *J Anim Ecol.* 2005; 74: 1195–1198. <https://doi.org/10.1111/j.1365-2656.2005.01005.x>
11. Oro D. Seabirds and climate: knowledge, pitfalls, and opportunities. *Front Ecol Evol.* 2014; 2:79. <https://doi.org/10.3389/fevo.2014.00079>
12. Ottersen G., Planque B., Belgrano A., Post E., Reid P.C. & Stenseth N.C. Ecological effects of the North Atlantic Oscillation. *Oecologia.* 2001; 128: 1–14. <https://doi.org/10.1007/s004420100655> PMID: 28547079

13. Stenseth N.C., Ottersen G., Hurrell J.W., Myrseth A., Lima M., Chan K.-S., et al. Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. 2003; *Proc R Soc Lond B Biol Sci.* 270: 2087–2096. <https://doi.org/10.1098/rspb.2003.2415>
14. Frederiksen M., Harris M.P., Daunt F., Rothery P. & Wanless S. Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob Change Biol.* 2004; 10: 1214–1221. <https://doi.org/10.1111/j.1529-8817.2003.00794.x>
15. McKinney M. A., Iverson S. J., Fisk A. T., Sonne C., Rigét F. F., Letcher R. J., et al. Global change effects on the long-term feeding ecology and contaminant exposures of East Greenland polar bears. *Glob Change Biol.* 2013; 19(8): 2360–2372. <https://doi.org/10.1111/gcb.12241> PMID: 23640921
16. Ferguson S. H., Young B. G., Yurkowski D. J., Anderson R., Willing C., & Nielsen O. Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. *PeerJ.* 2017; 5: e2957. <https://doi.org/10.7717/peerj.2957> PMID: 28168119
17. Drinkwater K.F., Belgrano A., Borja A., Conversi A., Edwards M., Greene C.H., et al. The Response of Marine Ecosystems to Climate Variability Associated with the North Atlantic Oscillation. In *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*. Geophysical Monograph 134: American Geophysical Union; 2003. <https://doi.org/10.1029/134GM10>.
18. Genovart M., Sanz-Aguilar A., Fernández-Chacón A., Igual J.M., Pradel R., Forero M.G., et al. Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. *J Anim Ecol.* 2013; 82: 121–130. <https://doi.org/10.1111/j.1365-2656.2012.02015.x> PMID: 22823099
19. Mesquita M.dS., Erikstad K.E., Sandvik H., Barrett R.T., Reiertsen T.K., Anker-Nilssen T. et al. There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird. *Front Ecol Evol.* 2015; 3, 43. <https://doi.org/10.3389/fevo.2015.00043>
20. Eriksson M.O.G. Prey Detectability for Fish-Eating Birds in Relation to Fish Density and Water Transparency. *Ornis Scand.* 1985; 16: 1–7. <https://doi.org/10.2307/3676567>
21. Butler S.J. & Gillings S. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis.* 2004; 146(s2): 123–130. <https://doi.org/10.1111/j.1474-919X.2004.00352.x>
22. Butler S.J., Bradbury B. & Whittingham M.J. Stubble height affects the use of stubble fields by farmland birds. *J App Ecol.* 2005; 42: 469–476. <https://doi.org/10.1111/j.1365-2664.2005.01027.x>
23. Vaughn R., Worsig B., Shelton S., Timm L.L. & Watson, L.A. Dusky dolphins influence prey accessibility for seabirds in Admiralty Bay, New Zealand. *J Mammal.* 2008; 89(4): 1051–1058. <https://doi.org/10.1644/07-MAMM-A-145.1>
24. Oro D. & Ruiz X. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. *ICES J Mar Sci.* 1997; 54: 695–707. <https://doi.org/10.1006/jmsc.1997.0246>
25. Abello P. & Oro D. Offshore distribution and assemblages of breeding seabirds in the Catalano-Balearic Sea (northwestern Mediterranean). *Colonial Waterbirds.* 1998; 21: 422–426.
26. Martínez-Abraín A., Maestre R. & Oro D. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. *ICES J Mar Sci.* 2002; 59: 529–537. <https://doi.org/10.1006/jmsc.2001.1175>
27. Bécares J., Arcos J.M. & Oro D. Migración y Ecología Espacial de la gaviota de Audouin en el Mediterráneo Occidental y Noroeste Africano. Monografía n.º1 del programa Migra; 2016.
28. De los Reyes González J.M., Zajková Z., Virginia, Morera-Pujol V., De Felipe F., Militão T., et al. Migración y ecología espacial de las poblaciones de Pardela Cenicienta. *Quercus.* 2017; 391: 26–32.
29. Cunningham E. Russell, A. Sex differences in avian yolk hormone levels. *Nature.* 2001; 412: 498. <https://doi.org/10.1038/35087655>.
30. Christians J.K. Avian egg size: variation within species and inflexibility within individuals. *Biol Rev Camb Philos Soc.* 2002; 77: 1–26. <https://doi.org/10.1017/s1464793101005784> PMID: 11911371
31. Oro D. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. *Mar Ecol Prog Ser.* 1996; 132: 43–46. <https://doi.org/10.3354/meps132043>
32. Oro D., Jover L.I., Ruiz X. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's Gull *Larus audouinii*. *Mar Ecol Prog Ser.* 1996; 139: 19–29. <https://doi.org/10.3354/meps139019>
33. Real E., Oro D., Martínez-Abraín A., Igual J.M., Bertolero A., Bosch M., et al. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. *J Avian Biol.* 2017; 48: 1462–1470. <https://doi.org/10.1111/jav.01454>

34. Parsons J. Relationship between egg size and post-hatching chick mortality in the herring gull (*Larus argentatus*). *Nature* 1970; 228: 1221–1222. <https://doi.org/10.1038/2281221a0> PMID: 5487258
35. Bolton M. Determinants of Chick Survival in the Lesser Black-Backed Gull: Relative Contributions of Egg Size and Parental Quality. *J Anim Ecol*. 1991; 60: 949–960. <https://doi.org/10.2307/5424>
36. Blomqvist D., Johansson O.C. & Götmark F. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia*. 1997; 110: 18–24. <https://doi.org/10.1007/s004420050128>
37. Risch T.S. & Rohwer F.C. Effects of parental quality and egg size on growth and survival of herring gull chicks. *Can J Zool*. 2000; 78: 967–973. <https://doi.org/10.1139/z00-029>
38. Hoyt D.F. Practical Methods of estimating volume and fresh weight of bird eggs. *Auk*. 1979; 96: 73–77.
39. Louzao M., Igual J.M., Genovart M., Forero M.G., Hobson K.A., Oro D. Spatial variation in egg size of a top predator: Interplay of body size and environmental factors?. *Acta Oecol*. 2008; 34: 186–193. <https://doi.org/10.1016/j.actao.2008.05.007>
40. Dunn E.K. Changes in Fishing Ability of Terns associated with Wind speed and Sea Surface Conditions. *Nature*, 1973; 244: 520–521. <https://doi.org/10.1038/244520a0>
41. Baptist M.J. & Leopold M.F. Prey capture success of Sandwich Terns *Sterna sandvicensis* varies non-linearly with water transparency. *Ibis*. 2010; 152: 815–825. <https://doi.org/10.1111/j.1474-919X.2010.01054.x>
42. Sanz-Aguilar A., Igual J.M., Oro D., Genovart M. & Tavecchia G. Estimating recruitment and survival in partially monitored populations. *J App Ecol*. 2016; 53: 73–82. <https://doi.org/10.1111/1365-2664.12580>
43. Morote E., Olivar M.P., Villate F. & Uriarte I. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. *ICES J Mar Sci*. 2010; 67: 897–908. <https://doi.org/10.1093/icesjms/fsp302>
44. Tugores M.P., Iglesias M., Díaz N., Oñate D., Miquel J. & Giráldez A. Latitudinal and interannual distribution of the European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the western Mediterranean, and sampling uncertainty in abundance estimates. *ICES J Mar Sci*. 2010; 67: 1574–1586. <https://doi.org/10.1093/icesjms/fsq057>
45. Pedrocchi V., Oro D., González-Solís J., Ruiz X. & Jover L. Differences in diet between the two largest breeding colonies of Audouin's gulls: the effects of fishery activities. *Sci Mar*. 2002; 66, 3: 313–320. <https://doi.org/10.3989/scimar.2002.66n3313>
46. Alonso H., Granadeiro J.P., Paiva V.H., Dias A.S., Ramos J.A. & Catry P. Parent–offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. *Mar Biol*. 2012; 159: 1197–1207. <https://doi.org/10.1007/s00227-012-1900-2>
47. Alonso H., Granadeiro J.P., Dias M.P., Catry T. & Catry P. Fine-scale tracking and diet information of a marine predator reveals the origin and contrasting spatial distribution of prey. *Prog Oceanogr*. 2018; 162: 1–12. <https://doi.org/10.1016/j.poccean.2018.02.014>
48. Gaglione D., Cook T.R., McInnes A., Sherley R.B. & Ryan P.G. Foraging plasticity in seabirds: A non-invasive study of the diet of greater crested terns breeding in the Benguela region. *PLoS One*. 2018; 13: e0190444. <https://doi.org/10.1371/journal.pone.0190444> PMID: 29385167
49. Zuur A. Leno E.N. and Elphick C.S. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 2010; 1: 3–14. <http://www.respond2articles.com/MEE/>
50. Robinson Cecil & Schumacker Randall. Interaction Effects: Centering, Variance Inflation Factor, and Interpretation Issues. *MLRV*. 2009; 35: 6–11.
51. Burnham K.P. & Anderson D.R. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. Springer-Verlag: New York; 2002.
52. Burnham K.P. & Anderson D.R. Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociol Methods Res*. 2004; 33: 261–304. <https://doi.org/10.1177/0049124104268644>
53. Harris M.P., Anker-Nilssen T., McCleery R.H., Erikstad K.E., Shaw D.N. & Grosbois V. Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. *Mar Ecol Prog Ser*. 2005; 297: 283–296. <https://doi.org/10.3354/meps297283>
54. Anderson D.R. Model Based Inference in the Life Sciences: A Primer on Evidence. New York: Springer-Verlag; 2008.
55. Evans J.A. & Davis A.S. Consequences of parameterization and structure of applied demographic models: a comment on Pardini et al. 2009. *Ecol App*. 2011; 21: 608–613. <https://doi.org/10.1890/08-0845.1>
56. Harrison X.A., Blount J.D., Inger R., Norris D.R. & Bearhop S. Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol*. 2011; 80: 4–18. <https://doi.org/10.1111/j.1365-2656.2010.01740.x> PMID: 20726924

57. O'Connor C.M., Norris D.R., Crossin G.T. & Cooke S.J. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere*. 2014; 5(3): 1–11. <https://doi.org/10.1890/ES13-00388.1>
58. Philippi T. & Seger J. Hedging one's evolutionary bets, revisited. *Trends Ecol Evol*. 1989; 4: 41–44. [https://doi.org/10.1016/0169-5347\(89\)90138-9](https://doi.org/10.1016/0169-5347(89)90138-9) PMID: 21227310
59. Martínez-Asensio A., Tsimplis M.N., Marcos M., Feng X., Gomis D., Jordà G., et al. Response of the North Atlantic wave climate to atmospheric modes of variability. *Int J Climatol*. 2016; 36: 1210–1225. <https://doi.org/10.1002/joc.4415>
60. Hurrell J.W. & Deser C. North Atlantic climate variability: The role of the North Atlantic Oscillation Impact of climate variability on marine ecosystems: A comparative approach. *J Mar Syst*. 2010; 79: 231–244. <https://doi.org/10.1016/j.jmarsys.2008.11.026>
61. Arcos J.M., Oro D. & Sol D. Competition between the yellow-legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. *Mar Biol*. 2001; 139: 807–816. <https://doi.org/10.1007/s002270100651>
62. Daunt F., Afanasyev V., Silk J.R.D. & Wanless S. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behav Ecol Sociobiol*. 2006; 59: 381–388. <https://doi.org/10.1007/s00265-005-0061-4>
63. Fuller A.K., Harrison D.J. & Vashon J.H. Winter habitat selection by Canada lynx in Maine: Prey abundance or accessibility?. *Jour Wildl Manage*. 2010; 71(6): 1980–1986. <https://www.jstor.org/stable/4496293>
64. Hopcraft J. G. C., Sinclair A. R. E., & Packer C. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*. 2005; 74(3): 559–566. <https://doi.org/10.1111/j.1365-2656.2005.00955.x>
65. Louzao M., Gallagher R., García-Barón I., Chust G., Intxausti I., Albisu J., et al. Threshold responses in bird mortality driven by extreme wind events. *Ecol Indic*. 2019; 99: 183–192. <https://doi.org/10.1016/j.ecolind.2018.12.030>
66. Taylor I.R. Effect of Wind on the Foraging Behaviour of Common and Sandwich Terns. *Ornis Scand*. 1983; 14: 90–96. <https://doi.org/10.2307/3676011>
67. González-Solís J., Felicísimo A., Fox J.W., Afanasyev V., Kolbeinsson Y. & Muñoz J. Influence of sea surface winds on shearwater migration detours. *Mar Ecol Prog Ser*. 2009; 391: 221–230. <https://doi.org/10.3354/meps08128>
68. Navarro J. & González-Solís J. Environmental determinants of foraging strategies in Cory's shearwaters *Calonectris diomedea*. *Mar Ecol Prog Ser*. 2009; 378: 259–267. <http://dx.doi.org/10.3354/meps07880>
69. Matthiopoulos J. The use of space by animals as a function of accessibility and preference. *Ecol Model*. 2003; 159: 239–268. [https://doi.org/10.1016/S0304-3800\(02\)00293-4](https://doi.org/10.1016/S0304-3800(02)00293-4)
70. Velando A. & Freire J. Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain). *Mar Ecol Prog Ser*. 1999; 188: 225–236. <https://doi.org/10.3354/meps188225>
71. González-Solís J., Oro D., Jover L., Ruiz X. & Pedrocchi V. Trophic Niche Width and Overlap of Two Sympatric Gulls in the Southwestern Mediterranean. *Oecologia*. 1997; 112: 75–80. <https://doi.org/10.1007/s004420050285> PMID: 28307378
72. Genovart M., Oro D. & Tenan S. Immature survival, fertility, and density dependence drive global population dynamics in a long-lived species. *Ecology*. 2018; 99: 2823–2832. <https://doi.org/10.1002/ecy.2515> PMID: 30422304
73. Yalden D.W. & Pearce-Higgins J.W. Density-dependence and winter weather as factors affecting the size of a population of Golden Plovers *Pluvialis apricaria*. *Bird Study*. 1997; 44: 227–234. <https://doi.org/10.1080/00063659709461058>
74. Ottersen G., Ådlandsvik B. & Ingvaldsen R. Temperature variability in the Northeast Atlantic. *ICES J Mar Sci Symposia*. 2003; 219: 86–94.