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Teleconnection Between the Reproductive Parameters of the Bearded Vulture and Macroclimatic Oscillations: Implications for Conservation

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ABSTRACT.—The Bearded Vulture (*Gypaetus barbatus*) is a scavenging bird of prey that was once widespread on the Iberian Peninsula. Its current distribution in Spain is limited to specific mountain ranges, including the Aragonese Pyrenees. The decline of the Iberian population has been linked to factors acting at a microscale level, such as the use of poisons, illegal hunting, and a decrease in extensive livestock farming. There are, however, other factors acting on a biogeographical scale that are not currently being considered and may also be affecting the viability of populations. The aim of this case study was to investigate the influences of large-scale environmental conditions on temporal variation in the reproductive parameters of the Bearded Vulture breeding population in the Aragonese Pyrenees. We tested the degree to which each of 26 macroclimatic oscillation indices with an effect on regional weather conditions were teleconnected with three reproductive parameters (hatching rate, fledging rate, and productivity). Two indices—the Tropical Northern Atlantic and East Atlantic/West Russia Pattern—were temporally correlated with Bearded Vulture reproductive parameters. The study results provide novel information to facilitate Bearded Vulture conservation because no previous studies have addressed this issue from a biogeographical and macroecological perspective. The results could have important implications for the management and conservation of the species and its successful reintroduction in other territories.

KEY WORDS: *Conservation*; *favorability*; *modeling*; *vulture*; *weather conditions*.

TELECONEXIÓN ENTRE LOS PARÁMETROS REPRODUCTIVOS DE *GYPAETUS BARBATUS* Y LAS OSCILACIONES MACROCLIMÁTICAS: IMPLICACIONES PARA LA CONSERVACIÓN

RESUMEN.—*Gypaetus barbatus* es un ave de presa carroñera llegó a estar ampliamente distribuida en la Península Ibérica. Su distribución actual en España se limita a ciertas cadenas montañosas, incluyendo los Pirineos Aragoneses. La disminución de la población ibérica se ha relacionado con factores que actúan a nivel de microescala, como el uso de venenos, la caza ilegal y una disminución de la ganadería extensiva. Sin embargo, existen otros factores que actúan a una escala biogeográfica que actualmente no se están considerando y que también pueden estar afectando la viabilidad de las poblaciones. El objetivo de este estudio fue investigar la influencia de las condiciones ambientales a gran escala en la variación temporal de los parámetros reproductivos de la población reproductora de *G. barbatus* en los Pirineos Aragoneses. Evaluamos el grado en que cada uno de los 26 índices de oscilación macroclimática con efecto en las condiciones meteorológicas regionales estaban teleconectados con tres parámetros reproductivos (tasa de eclosión, tasa de emplumamiento y productividad). Dos índices—el Atlántico Norte Tropical y el Patrón Atlántico Este/Rusia Occidental—estaban correlacionados temporalmente con los parámetros reproductivos de *G. barbatus*. Los resultados del estudio proporcionan información novedosa

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para facilitar la conservación de *G. barbatus*, ya que ningún estudio previo ha abordado este tema desde una perspectiva biogeográfica y macroecológica. Los resultados podrían tener importantes implicaciones para la gestión y conservación de la especie y su reintroducción exitosa en otros territorios.

[Traducción del equipo editorial]

INTRODUCTION

The Bearded Vulture is a necrophagous bird specializing in an osteophagous diet (Margalida and Martínez 2020). It is found in mountain ranges with steep topography and rocky nesting sites, and forages on surrounding plains and plateaus with large open areas and little or low vegetation (Ferguson-Lees and Christie 2001, Orta et al. 2020). Bearded Vultures are distributed throughout mountainous regions of Eurasia and Africa (Orta et al. 2020). In the last century, the distribution of the Bearded Vulture was increasingly restricted due to both direct and indirect persecution, which reduced the species' current range to a few isolated massifs in the Pyrenees, Corsica, Greece, and the Balkans (Margalida and Martínez 2020). Recently, various conservation and reintroduction projects have helped to improve the overall status of Bearded Vultures by enabling the species to begin returning to territories it once occupied (Margalida and Martínez 2020).

The distribution and population dynamics of Bearded Vultures are conditioned by factors acting locally, such as illegal hunting, poisoning, power line collisions and electrocutions, human disturbance in breeding areas, abandonment of extensive livestock farming and the consequent decrease in trophic resources, and interspecific competition with Griffon Vultures (*Gyps fulvus*) for nesting sites (Margalida 2016, Gil 2020). On a wider geographical scale, the species' distribution is linked to and modified by specific environmental conditions (Vanderwal et al. 2013). Similarly, population dynamics are related to the meteorological conditions existing at certain points of the biological cycle (Kostin and Mooij 1995, Ramos et al. 2002, McDonald et al. 2004). Local weather conditions are concurrently controlled by remote macroclimatic atmospheric and oceanic circulatory patterns (Formenty et al. 2003), which are quantified by macroclimatic indices that support comparing time series to estimate means and identify extreme values and trends (Jiménez 2014). As a result of these relationships, temporal weather patterns can be described using indices derived from monitoring macroclimatic oscillations (Gordo et al. 2011), which ultimately trigger ecological processes affecting the population dynamics of species. Such links between ecosystem properties and distant climatic oscillation patterns, termed teleconnections (Heffernan et al. 2014), have been reported for other species (Báez et al. 2021, 2022). There is normally a time lag between macroclimatic oscillations and the ecological processes they activate. This could support advanced weather forecasting to provide advantages when planning management and conservation actions for Bearded Vultures.

In this study, we focused on understanding the relationship between the rates of macroclimatic oscillations and reproductive parameters of the main Bearded Vulture population in Europe. We first identified relevant oscillation indices related to reproduction of the species and associated response time lags. Our initial hypothesis was that Bearded Vulture breeding parameters are determined, at least in part, by weather patterns that can be anticipated by measuring certain macroclimatic indices. The underlying assumption was that macroclimatic indices determine local weather conditions, which affect breeding parameters and thus population dynamics. We developed a model to predict the degree to which the macroclimatic indices and, therefore, the consequent meteorological conditions, appeared to influence reproduction of Bearded Vultures during a 32-yr study period. The resulting insight can be used to improve management and conservation actions designed to better conserve the species.

METHODS

The geographical context of this study was the Aragonese Pyrenees in northern Spain (Fig. 1), where the main European population of Bearded Vultures is located (Margalida and Martínez 2020). The study area was delimited by the recovery plan for the species (General Council of Aragón 1994), covering 9537 km^2 and including Ordesa y Monte Perdido National Park, which is a UNESCO World Heritage Site. The database of reproductive parameters used in this study covered a 32-yr period from 1990–2021, with standardized annual monitoring begun in December when the earliest clutches were laid (Margalida et al. 2003). This population has been monitored since 1990 by the Government of Aragon and the Fundación para la Conservación del Quebrantahuesos (FCQ).

We created a database from a monitoring dataset provided by the FCQ and Government of Aragon

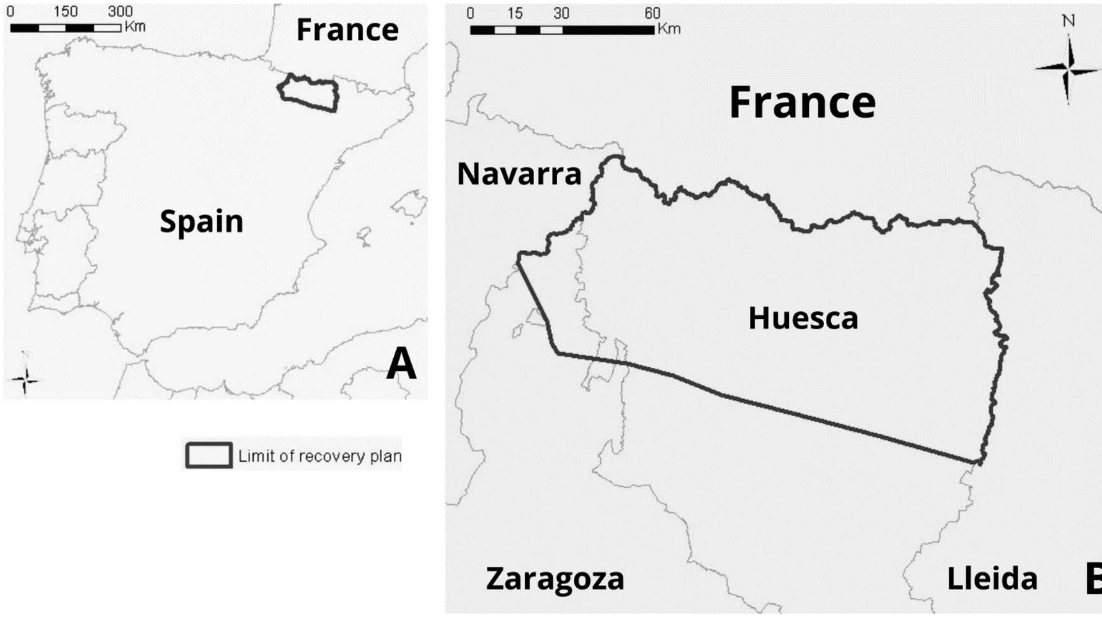

Figure 1. Study area. (A) Iberian Peninsula context; (B) Aragonese Pyrenees context.

that contained information about laying, hatching, and fledging for all reproductive units (i.e., an adult pair or a polyandrous group) in the study area and for each year of the study. We defined three annual reproductive parameters to serve as dependent variables for our analyses: (1) hatching rate = percentage of eggs that hatched; (2) fledging rate = number of nestlings that fledged/number of pairs with hatchlings; and (3) productivity = number of fledglings/number of successful pairs, where a successful pair was one that raised one nestling to fledgling. To differentiate between years with high and low values of these reproductive parameters, we established six intervals using a logarithmic scale for each reproductive parameter (Vargas et al. 2006, Farfán et al. 2012). We then considered values in the three highest intervals (≥ 0.7) as representative of high reproductive years and values in the three lower intervals (<0.7) as low reproductive years, thereby composing three binary response variables reflecting high and low years for each reproductive parameter.

Macroclimatic Oscillation Indices. We compiled information for 26 climate indices (Table 1) with data available from the National Oceanic and Atmospheric Administration (2023) and Indian Institute of Tropical Meteorology (2023). These indices are calculated on a monthly basis from measurements of different climate characteristics over time (Xiao 2020). Given that the oscillations in circulatory patterns could have a delayed teleconnection effect on Bearded Vulture reproductive parameters in the study area, we considered different possible features of the oscillation indices to represent temporal lags in our predictors (Stenseth et al. 2002, Báez et al. 2013). Specifically, as a predictor of high or low reproductive parameters, we tested average values of the oscillation indices from the quarter previous to the start of a given annual reproductive period (November–January), which is an appropriate period within which to identify management measures to be carried out.

Predictive Models. We trained predictive models for the three dependent variables for the period 1990–2021. We developed models of climatically favorable years using the favorability function described by Real et al. (2006):

$$F = \frac{\frac{P}{(1-P)}}{\left(\frac{n_1}{n_0}\right) + \left(\frac{P}{(1-P)}\right)}$$

where F is the meteorological favorability of the quarter previous to the start of the reproductive period (ranging from 0 to 1), P is the probability of occurrence of a high reproductive parameter value during the year, and n_1 and n_0 are the number of years during 1990–2021 with occurrence and absence of a high reproductive parameter value, respectively.

Table 1. Macroclimatic oscillation indices used to assess possible links with reproductive parameters of Bearded Vultures in the Pyrenees, Spain.

Index	Code	Index	Code
Atlantic Oscillation Index	AAO	Atlantic Meridional Mode	AMM
Atlantic Multidecadal Oscillation	AMO	Artic Oscillation Index	AO
East Atlantic Pattern	EA	Dipole Mode Index	DMI
East Pacific/North Pacific Pattern	EP/NP	East Atlantic/West Russia Pattern	EA/WR
North Atlantic Oscillation	NAO	Multivariate ENSO Index	MEI
East Central Tropical Pacific SST	NIÑO 34	Extreme Eastern Tropical Pacific SST	NIÑO 1 + 2
North Pacific Pattern	NP	Central Tropical Pacific SST	NIÑO 4
Oceanic Nino Index	ONI	North Tropical Atlantic SST Index	NTA
Polar/Eurasia Pattern	POL	Pacific/North American Pattern	PNA
Scandinavian Pattern	SCA	Quasi-Biennial Oscillation	QBO
Tropical Northern Atlantic Index	TNA	Southern Oscillation Index	SOI
Tropical Southern Atlantic Index	TSA	Tropical/Northern Hemisphere Pattern	TNH
West Pacific Pattern	WP	Western Hemisphere Warm Pool	WHWP

Models based on the favorability function identified with $F > 0.5$ indicate years with weather conditions that caused the probability of high reproductive parameter values to be higher than the prevalence of these events in the temporal dataset (Acevedo and Real 2012). We obtained probability values using logistic regression to relate each binary dependent variable to the macroclimatic oscillation indices (Hosmer and Lemeshow 2000).

We derived logistic regression parameters by maximum likelihood estimation using a gradient-ascent, machine-learning algorithm (Schein and Ungar 2007, Rymarczyk et al. 2019). To minimize multicollinearity between predictors, we grouped predictor variables with significant Spearman correlation coefficients and for each group retained only the variable demonstrating the strongest relationship with the dependent variables. We generated ensemble forecasting models based on the assumption that the effects of the different uncorrelated predictors are additive (Romero et al. 2016). We conducted multivariate logistic regression analyses of each dependent variable on the subset of retained predictors using a forward-backward stepwise approach. This stepwise process identified the most significant model with only one predictor based on Rao's score test (Rao 2005), and then sequentially added other predictors that significantly improved the model based on the omnibus test (Hosmer and Lemeshow 2000). We used Wald tests (Freund 1993) to assess the relative contributions of each predictor in the multivariate models.

We classified each study year as favorable or unfavorable for the occurrence of high reproductive parameter values using $F = 0.5$ as the favorability threshold according to each model. Then we used six indices to evaluate the classification capacity of each model: (1) sensitivity = proportion of high reproductive years classified as favorable; (2) specificity = proportion of low reproductive years classified as unfavorable; (3) correct classification rate = proportion of years correctly classified as favorable or unfavorable based on high versus low reproductive parameters, respectively; (4) over-prediction = proportion of years classified as favorable that presented low reproductive parameter values; (5) under-prediction = proportion of years classified as unfavorable that presented high reproductive parameters; and (6) Cohen's kappa coefficient = proportion of specific agreement between the occurrence of high or low reproductive parameter values and favorability classifications (Fielding and Bell 1997). To assess the overall discrimination capacity of the models, we also used estimates of the area under receiver operating characteristic curve (AUC) as a measure independent of favorability thresholds (Lobo et al. 2008). We used the Hosmer and Lemeshow's goodness-of-fit test (Hosmer and Lemeshow 2000) to assess calibration.

RESULTS

Eleven of 32 yr had high hatching rates, 17 yr had high fledging rates, and 13 yr had high productivity values. We obtained significant climatic favorability models for all dependent variables (Tables 2 and 3). The Tropical Northern Atlantic (TNA) index was significantly and negatively associated with the likelihood of obtaining high values of all three reproductive parameters (Table 2). The average TNA index during the quarter prior to the

Table 2. Parameters and test statistics for significant logistic regression models relating reproductive variables for Bearded Vultures in the Pyrenees, Spain, to macroclimatic oscillation indices. Logits represent either univariate models or multivariate combinations under the assumption that the individual effects of uncorrelated predictors would be additive.

Dependent Variable[a]	Predictor[b]	Constant	β[c]	Wald Statistic[d]	*P*
Hatching rate	TNA	−0.069	−2.886	3.732	0.053
Fledge rate	TNA	1.024	−3.664	5.394	0.020
Productivity	TNA	1.011	−6.341	6.677	0.010
	EA/WR	—	1.650	3.925	0.048

[a] Hatching rate: percentage of eggs that hatched; fledging rate: number of nestlings that fledged/pair with hatchlings; productivity: total number of fledglings/total number of pairs.
[b] TNA = Tropical Northern Atlantic; EA/WR = East Atlantic/Western Russia.
[c] Predictor coefficient.
[d] Wald test value quantifying predictor weight in model.

November–January reproductive period was positive in 23 yr (72%) and negative in 9 yr (28%; Fig. 2A). High hatching rates, fledging rates, and productivity occurred in 4 yr (36%), 9 yr (53%), and 5 yr (39%) after quarters with negative TNA values, respectively. High reproductive parameter values were favored ($F > 0.5$) by TNA values ≤ 0.2 in the quarter prior to the reproductive period (Fig. 2B–D).

The East Atlantic/West Russia Pattern (EA/WR) index was the other informative macroclimatic oscillation index. The averaged values during the quarter prior to the reproductive period were significantly and positively associated with the likelihood of obtaining high productivity values (Fig. 3A). The EA/WR index in the quarter prior to the reproductive period was positive in 13 of 32 yr (41%) and negative in 19 yr (59%). High productivity occurred in 6 yr (46%) after quarters with positive EA/WR index values and was favored ($F > 0.5$) by positive values of the EA/WR index in the quarter prior to the reproductive period (Fig. 3B).

DISCUSSION

Our study results suggest that Bearded Vulture reproductive parameter values are teleconnected with two macroclimatic oscillation indices. From the perspective of environmental sciences, teleconnection refers to any phenomenon that creates links between distant and otherwise disconnected regions (Heffernan et al. 2014), including the link between ecosystem features and distant global circulation patterns. This implies the existence of macroclimatic patterns of meteorological effects that could trigger ecosystem changes favoring, or not, reproduction of Bearded Vultures.

It is well known that the Pyrenean Bearded Vulture population is strongly affected by a phenomenon of negative density-dependence (Margalida and Martínez 2020), along with other factors that also act on a local scale, such as human disturbance, poisoning, or illegal hunting (Margalida 2016, Gil 2020). It is essential, however, to also know about other factors that, acting on a larger biogeographical scale, may also be conditioning the reproductive parameters and, ultimately, viability of the population. As our results show, the TNA index appears to be the most important macroclimate driver of reproductive parameters for the Bearded Vulture in the study area. The TNA index is an indicator of ocean surface temperatures in the eastern tropical North Atlantic Ocean, mainly associated with thermodynamic air-sea interactions (Huang 2004). Several authors have shown that the TNA index has a clear influence on weather conditions in many regions. For instance, variations in precipitation in the Caribbean and in northeastern Brazil are closely related to changes in the TNA index (Uvo et al. 1998, Enfield and Alfaro 1999), and precipitation in southeastern Europe and East Asia is strongly correlated with the TNA index (Chen et al. 2018, Li et al. 2018). In our study area, positive TNA values are associated with frequent and severe droughts, whereas negative TNA values are associated with opposite trends (International Centre for Theoretical Physics 2011, Souza and Reboita 2021). Consequently, our results (which show that negative TNA index values correlate with the occurrence of high reproductive parameters) are consistent with the existing literature on Bearded Vultures, which states that reproduction is adversely affected by prolonged drought and is favored by moderate rainfall and temperatures (Margalida 2016). Our results

Table 3. Classification and discrimination measures of significant logistic climatic favorability models relating high-low reproductive parameters to macroclimatic oscillation indices for Bearded Vultures in Spain.

	Test Statistic							
Dependent Variable[a]	AUC[b]	Kappa[c]	Sensitivity[d]	Specificity[e]	Correct Classification Rate	Over-prediction[f]	Under-prediction[g]	H-L[h]
Hatching rate	0.701	0.188	0.636	0.571	0.594	0.563	0.250	$\chi^2 = 4.317$, $P = 0.634$
Fledging rate	0.859	0.502	0.706	0.800	0.750	0.200	0.294	$\chi^2 = 3.021$, $P = 0.082$
Productivity	0.870	0.680	0.846	0.842	0.844	0.214	0.111	$\chi^2 = 5.324$, $P = 0.503$

[a] Hatching rate: percentage of eggs that hatched; fledging rate: number of nestlings that fledged/pair with hatchlings; productivity: total number of fledglings/total number of successful pairs.

[b] Area under receiver operating characteristic curve.

[c] Cohen's kappa coefficient.

[d] Proportion of high reproductive years classified as favorable.

[e] Proportion of low reproductive years classified as unfavorable.

[f] Proportion of years classified as favorable that presented low reproductive parameter values.

[g] Proportion of years classified as unfavorable that presented high reproductive parameters.

[h] Hosmer-Lemeshow calibration index.

indicate that TNA index values from the quarter preceding the November–January reproductive period are good predictors of these conditions during the critical period for successful Bearded Vulture reproduction in the study area.

The other informative index (EA/WR) is driven by stationary eddy advection and transient eddy vorticity fluxes, and affects weather patterns from eastern North America to Eurasia (Franzke and Feldstein 2005, Lim 2015). In the Mediterranean region, Krichak et al. (2013) showed how the frequency of extreme precipitation is closely correlated with the EA/WR Pattern, whereas in East Asia it has a role in modulating winter-monsoon variability (Kim et al. 2013). In our study area, positive EA/WR values are associated with moderate rainfall and temperatures, whereas negative EA/WR values are associated with very low temperatures and excess precipitation (World Climate Service 2021). Again, our results regarding productivity being favored by positive EA/WR values coincide with the specialized literature on meteorological conditions that favor the reproductive biology of Bearded Vultures (Margalida 2016).

Conservation measures currently being carried out to benefit Bearded Vultures include reducing damage due to accidents, maintaining extensive livestock farming, creating and maintaining supplementary feeding points, and marking and monitoring individuals (López-Sañudo et al. 2001, Ferrer et al. 2014, Margalida and Martínez 2020). One of the measures currently being carried out with the aim of achieving a stable population includes extracting egg clutches from nests with a high risk of failure, captive breeding, and reintroduction in territories from which the Bearded Vulture was previously extirpated, such as at Picos de Europa and Maestrazgo (Margalida and Martínez 2020). Having information about the weather conditions expected during the reproductive period can be a useful tool for making decisions about which nests to act on. This approach can be achieved from the biogeographical perspective addressed in this study. The models based on teleconnections with macroclimatic oscillation indices can be the basis for making specific management decisions aimed to improve population viability. Conservation objectives for threatened species will be favored if we can forecast in advance the weather conditions expected during upcoming reproduction periods, or if we can anticipate extreme weather events that are becoming more frequent given global climate change.

In addition, the information provided by these teleconnection models can complement insights

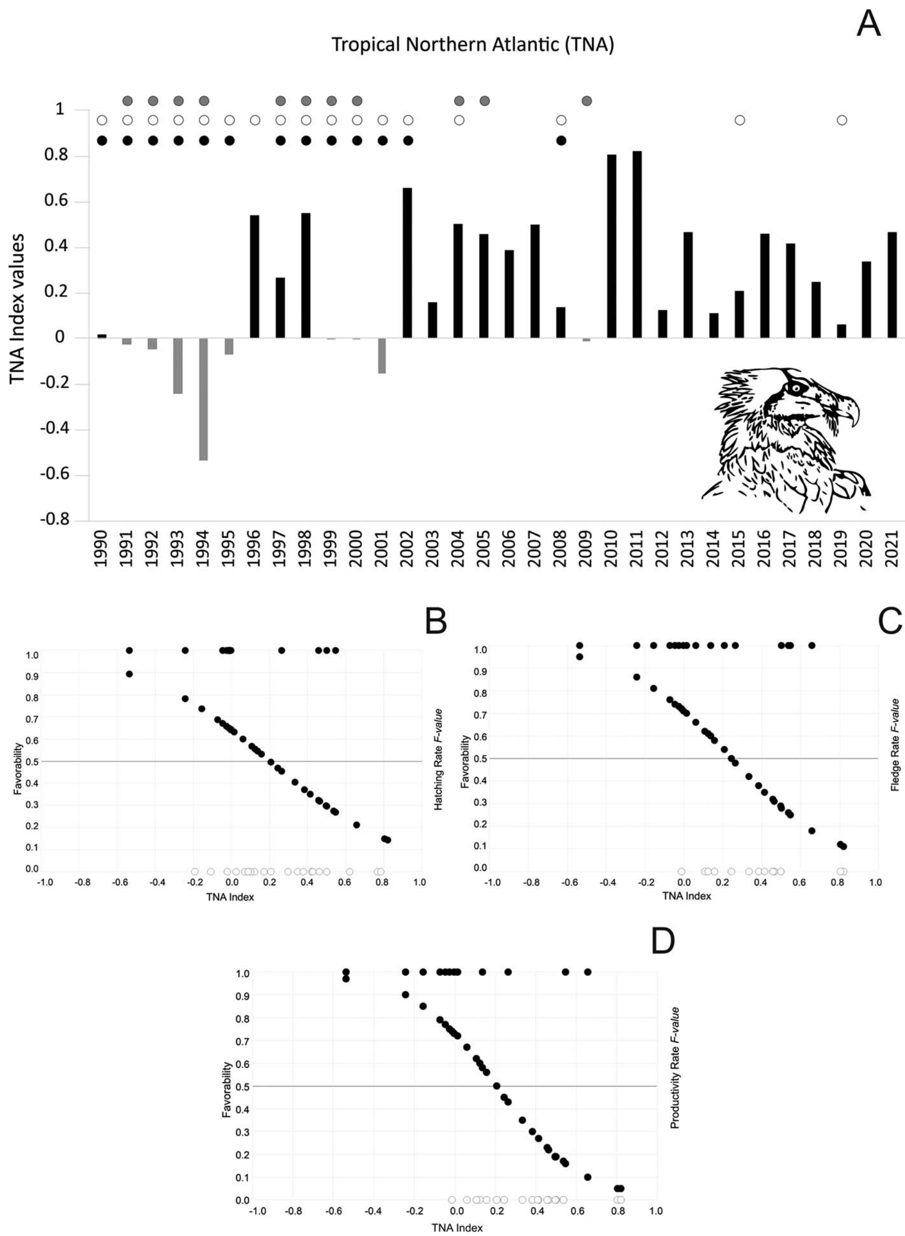

Figure 2. (A) Variation of the Tropical Northern Atlantic (TNA) macroclimatic oscillation index during the quarter prior to the November–January reproductive period and occurrence of high reproductive parameters (grey circle: high hatching rate; white circle: high fledging rate; black circle: high productivity) for Bearded Vultures from 1990–2021. (B) Hatching; (C) fledging; and (D) productivity. Relationship between climatic favorability (*F*-values) for the occurrence of high reproductive parameters and TNA values during the quarter prior to the November–January reproductive period. Black circles at the top: meteorological years with high values for (B) hatching, (C) fledging, and (D) productivity. White circles at the bottom: meteorological years with low values for (B) hatching, (C) fledging, and (D) productivity.

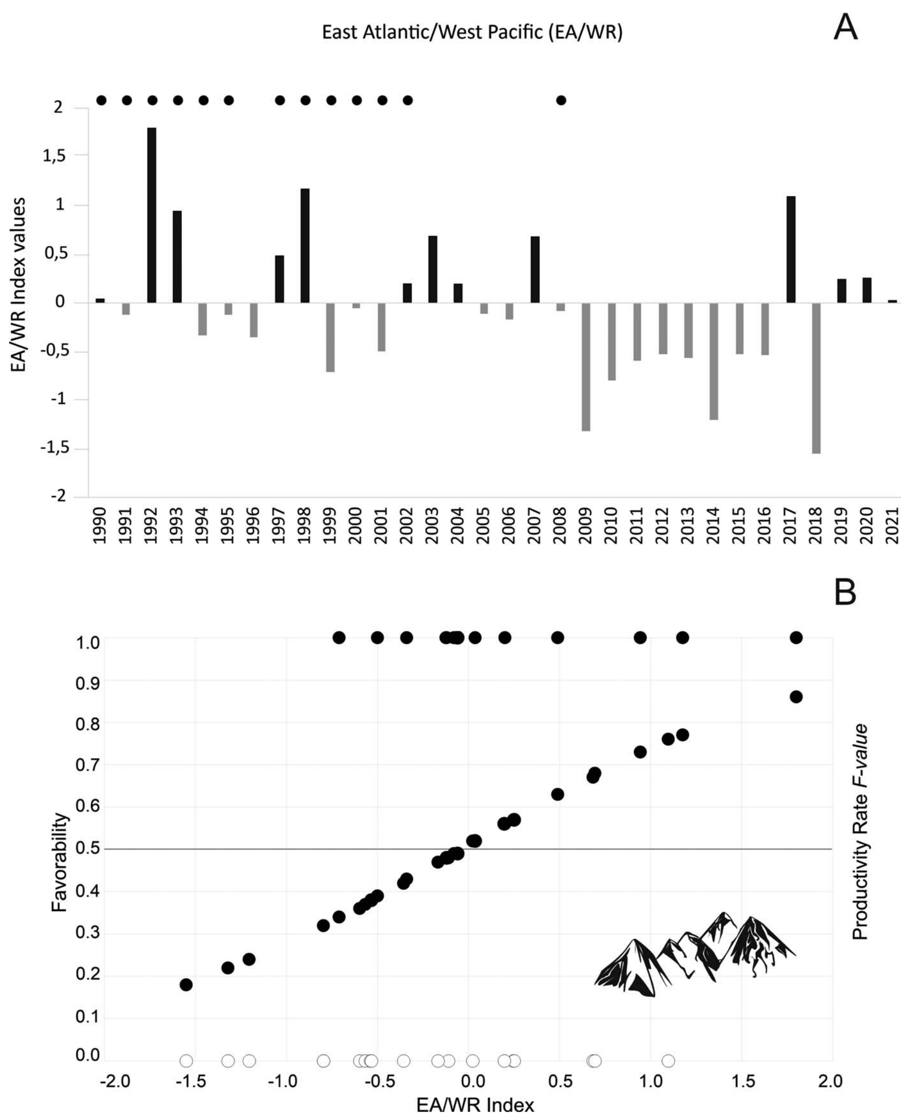

Figure 3. (A) Variation of East Atlantic/West Russia Pattern (EA/WR) macroclimatic oscillation index during the quarter prior to the November–January reproductive period and occurrence of high productivity (black circles) of Bearded Vultures from 1990–2021. (B) Relationship between climatic favorability (*F*-values) for the occurrence of high productivity and EA/WR values during the quarter prior to the November–January reproductive period. Black circles at the top: meteorological years with high values for productivity (B). White circles at the bottom: meteorological years with low values for productivity (B).

obtained from species distribution models, which relate a species' geographical distribution to multiple factors (e.g., historical, topographical, environmental, anthropogenic; Muñoz and Real 2006, Acevedo et al. 2011, Olivero et al. 2017). The combined use of these biogeographic tools could enable the adoption of specific management measures, such as egg removal for *ex situ* incubation, based on forecasts of unfavorable weather conditions. Our results could also complement distribution models that identify the most favorable areas for species and their carrying capacity (Muñoz et al. 2005, 2021), thereby supporting the selection of favorable reintroduction locations.

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