

Global climate patterns explain range-wide synchronicity in survival of a migratory seabird

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Abstract

To predict the impact of climate change over the whole species distribution range, comparison of adult survival variations over large spatial scale is of primary concern for long-lived species populations that are particularly susceptible to decline if adult survival is reduced. In this study, we estimated and compared adult survival rates between 1989 and 1997 of six populations of Cory's shearwater (*Calonectris diomedea*) spread across 4600 km using capture–recapture models. We showed that mean annual adult survival rates are different among populations along a longitudinal gradient and between sexes. Variation in adult survival is synchronized among populations, with three distinct groups: (1) both females and males of Corsica, Tremiti, and Selvagem (annual survival range 0.88–0.96); (2) both females and males of Frioul and females from Crete (0.82–0.92); and (3) both females and males of Malta and males from Crete (0.74–0.88). The total variation accounted for by the common pattern of variation is on average 71%, suggesting strong environmental forcing. At least 61% of the variation in survival is explained by the Southern Oscillation Index fluctuations. We suggested that Atlantic hurricanes and storms during La Niña years may increase adult mortality for Cory's shearwater during winter months. For long-lived seabird species, variation in adult survival is buffered against environmental variability, although extreme climate conditions such as storms significantly affect adult survival. The effect of climate at large spatial scales on adult survival during the nonbreeding period may lead to synchronization of variation in adult survival over the species' range and has large effects on the meta-population trends. One can thus worry about the future of such long-lived seabirds species under the predictions of higher frequency of extreme large-scale climatic events.

Keywords: adult survival, capture–recapture models, climate, Cory's shearwater, Southern Oscillation, synchrony

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Introduction

The global climate is warming, with important consequences for animal and plant populations (Walther

et al., 2002). Population changes are caused by variation in vital rates (demographic parameters), and many long-lived species have low population growth rates resulting from their life histories (small litter size, late recruitment, and high adult survival; Stearns, 1992). Population growth rates for long-lived species are strongly influenced by adult survival (Lebreton & Clobert, 1990). Adult survival may vary little, because

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variability is selectively disadvantageous for long-lived iteroparous species, and the variability of vital rates that has greatest impact on the population growth rate should be low (i.e. environmental canalization process; Saether & Bakke, 2000; Gaillard & Yoccoz, 2003).

Adult survival of long-lived species is affected by climate variation (e.g. Jenouvrier *et al.*, 2003). The effect of climate may vary within a year according to the life history of the species (e.g. breeding and wintering seasons; see Jenouvrier *et al.*, 2005), and may depend on the severity of environmental change at these different times of the year. Extreme climate events may particularly reduce adult survival, ultimately causing the population to crash (e.g. emperor penguin *Aptenodytes forsteri*, Jenouvrier *et al.*, 2005; barn owl *Tyto alba*, Altwegg *et al.*, 2006).

Climate effects could be critical during the nonbreeding season for long-lived migratory species when individuals from a wide range of breeding populations migrate to a same area, because any reduction in adult survival will cause a decrease in the whole metapopulation. Moreover, climatic influence during the nonbreeding season may cause synchrony in adult survival variability between breeding populations over a large spatial range (Harris *et al.*, 2005; Schaub *et al.*, 2005), and potentially increase the risk of species extinction (Royama, 1992). Therefore, comparison of adult survival variations over a wide spatial range is of primary concern to study the influence of climate on populations, and hence predict the impact of climate changes over the whole species distribution range.

Comparative studies focusing on variation in the vital rates within a species and covering a substantial part of the species' range are very rare (Frederiksen *et al.*, 2005). Most of the comparative studies to date compare previously published data (e.g. Frederiksen *et al.*, 2005). Few species are studied at the individual level with capture–recapture in population across their geographical range, to provide a rigorous joint analysis of original data from all sites (but see Harris *et al.*, 2005). Here, we compared the variation of adult survival of a procellariiform seabird (i.e. petrel), the Cory's shearwater (*Calonectris diomedea*), over a substantial range of its distribution. We estimated adult survival with a joint analysis from the original capture–recapture data for six breeding populations over 4600 km apart during 9 years.

Adult survival of several petrel species is affected by climate variability (e.g. Jenouvrier *et al.*, 2003), and also other factors that may interact with the effect of climate variability, such as sex (e.g. Jenouvrier *et al.*, 2005), density dependence (Barbraud & Weimerskirch, 2003), and fisheries (Rolland *et al.*, 2008). For Cory's shearwater, several potential nonexclusive factors may affect

adult survival, including physical factors (e.g. large climatic oscillation; Brichetti *et al.*, 2000), biological factors related to the environment (e.g. oceanographic productivity), factors specific to the species (e.g. sex, body size, and migration pattern), and finally human factors (harvesting and fisheries bycatch). Because seabird activity varies with season, these different factors may act at different spatial scales and time periods within a year. We first compared the average Cory's shearwater annual adult survival between the six populations and between sexes. The Cory's shearwater is sexually dimorphic (Ristow & Wink, 1980) and differences between sexes are thus expected. Moreover, we expect a longitudinal gradient in adult survival due to geographical variation in ocean productivity (Margalef, 1985; Caddy *et al.*, 1995; Freudenthal *et al.*, 2002), body size (Rabouam *et al.*, 1998), and migration patterns (Ristow *et al.*, 2000). Human impacts on adult survival also differed between the breeding sites; Cory's shearwater is harvested in the Sicily channel and is commonly fisheries bycatch in the Mediterranean (Belda & Sánchez, 2001).

Secondly, we studied temporal variability in adult survival. During the breeding season, the potential factors affecting survival involve specific local processes. Because the six breeding populations studied here are spread over 4600 km, we expect differences in temporal variation among populations if environmental conditions affect survival mainly during the breeding season. During the nonbreeding season, seabirds have a widespread distribution across vast oceanic ranges and can simply select a different area with better climate or trophic conditions (Harris *et al.*, 2005). Therefore, during the nonbreeding season, factors affecting adult survival variations are likely extreme events occurring at large spatial scales. Such events have the potential to result in synchrony in time series of adult survival (Schaub *et al.*, 2005). Moreover, we expect little variability in adult survival under the environmental canalization hypothesis (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003), although it would be surprising if adverse climate and trophic conditions did not affect survival at all. For instance, many seabird wrecks (i.e. large numbers of seabirds washing ashore) appear to be related to periods of stormy weather (Hudson, 1985).

Finally, we studied the potential influence of large-scale climate oscillations on temporal adult survival variations. Causal relationships between adult survival and large-scale climatic phenomena are not easily identified (Sandvik *et al.*, 2005), although large-scale climatic oscillations are remarkably good predictors of ecological responses to climate (Hallett *et al.*, 2004). Large-scale climatic oscillations are defined as temporal

fluctuations of pressure anomalies, and are treated as a 'proxy' for different climatic processes (Stenseth *et al.*, 2003). Large-scale climatic oscillations affect the local climate and oceanographic constraints (Ottersen *et al.*, 2001) and thus may affect adult survival of long-lived species directly by increasing mortality during extreme environmental events (e.g. Brichetti *et al.*, 2000), or indirectly through its effect on the abundance and distribution of prey (e.g. Sandvik *et al.*, 2005). We tested whether variability in adult survival is driven by large-scale climatic processes through direct or indirect effects. Atlantic hurricanes and storms during La Niña years of the Southern Oscillation (SO) may affect directly adult survivorship by increasing the mortality of migrating birds (Brichetti *et al.*, 2000). The North Atlantic Oscillation (NAO) may affect indirectly adult survivorship by its effect on the food web (Stenseth *et al.*, 2004).

Material and methods

Study species and sites

Cory's shearwaters are typical long-lived seabirds, with low fecundity (a single egg is laid per year), low first-year survival (Jenouvrier *et al.*, 2008), and delayed sexual maturity (see review in Thibault *et al.*, 1997; Mougin *et al.*, 2000; Jenouvrier *et al.*, 2008). The Cory's shearwater is sexually dimorphic (Ristow & Wink, 1980), and there are sex differences in vocalizations (Bretagnolle & Lequette, 1990). They forage at sea and feed on fish, molluscs, and offal (Sarà, 1993). They breed on islands and cliffs from the end of February to mid-October. Data on their wintering range are scarce, but observations suggest that the wintering area is very large and encompasses the entire Atlantic, potentially reaching the Indian Ocean (Thibault *et al.*, 1997). Birds from Atlantic populations seem to winter more westward in the Atlantic than those from the Mediterranean (Ristow *et al.*, 2000), although they are both observed in similar areas in different abundances (Camphuysen & Van Der Meer, 2001).

Studies were carried out on six breeding populations of Cory's shearwater on six islands from the eastern Atlantic to the eastern Mediterranean (Fig. 1). At the western and eastern edges of the Cory's shearwater breeding distribution range, the population number at Selvagem Island is the highest (30 000 birds) and at Crete the lowest (500–700 birds).

Data collection

In each population, birds were caught in their burrows or at the burrow's entrance and ringed. In subsequent

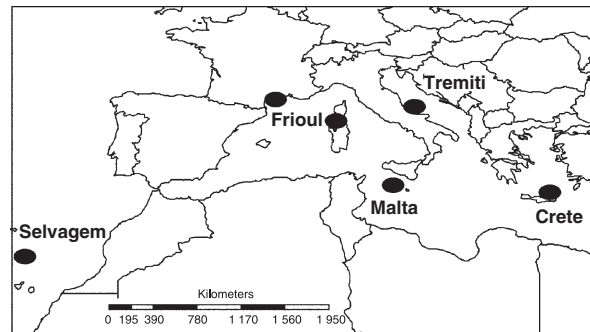


Fig. 1 Map of the study sites of the six studied populations of Cory's shearwater.

years, they were recaptured intensively in annually visited plots. The period of capture–recapture differed among population, because the present comparison was not intended when the authors independently started their fieldwork.

Birds were sexed on the basis of voice, bill measurements (length and height), or the sex of their breeding partner. Cory's shearwater body size decreases gradually eastward from the Atlantic to the Mediterranean (Thibault *et al.*, 1997; Rabouam *et al.*, 1998). Weight is used as a proxy of body size, although weight variations are influenced by stomach contents and fat stores, and thus showed important variations within a population.

Environmental variables

We tested the effect of Southern Oscillation Index (SOI) available at <http://www.cru.uea.ac.uk/cru/data/soi.htm> and the NAO (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) on adult survival of Cory's shearwater. The SO is a large-scale oscillation in atmospheric mass between the southeastern (Darwin) and southwestern (Tahiti) Pacific waters, and the NAO between the subtropical high (Azores) and the polar low (Iceland). We used the annual indices averaged over the entire year for SOI, because previous time series analysis detected strong annual variation and no significant seasonal variability in the SOI fluctuations (unpublished results), and over winter for the NAO (Stenseth *et al.*, 2004).

The effect of the SO is most pronounced in the southeastern Pacific Ocean, although other marine ecosystems are also affected, such as the Southern Atlantic (e.g. Duffy, 1990) where Cory's shearwaters spend the winter. Sustained negative values of the SOI indicate El Niño episodes, while positive values indicate La Niña episodes. La Niña episodes favor tropical storms and

hurricanes in the Atlantic that likely influence the survivorship of Cory's shearwaters by causing increased heat loss, displacing birds to areas with less food, or making foraging more difficult because common fish prey species move deeper into the water column (Brichetti *et al.*, 2000).

The NAO may affect seabird mortality directly (wind) and/or indirectly (prey availability), although several studies suggest that these effects are indirect rather than direct (Harris *et al.*, 2005; Sandvik *et al.*, 2005). In our case, because birds wintered in the Southern Atlantic and the equatorial zone, a direct effect of the NAO on mortality is not expected because the storms occur in the North Atlantic Ocean. NAO may affect seabird mortality during the breeding season through its lagged effects on the abundance of lower trophic level species (e.g. phytoplankton, zooplankton, and fish; Stenseth *et al.*, 2004). Because Cory's shearwaters forage on lower trophic species with short life cycle, lags are expected to be seasonal rather than yearly. Therefore, we assumed a lag of one season, and we used the NAO during winter to test its effect on adult survival during the following breeding season.

Data analysis and modeling

The analysis is based on capture–recapture histories of birds of unknown age when ringed, and recaptured in the subsequent years as breeders from populations where the same burrows have been checked each year. Datasets differed in length, and the analysis was restricted to the common period from 1989 to 1997.

We used capture–mark–recapture (CMR; Lebreton *et al.*, 1992) models to estimate adult annual survival rates. CMR models distinguish survival (noted Φ), defined as the probability that a shearwater alive at year t survives at year $t + 1$, and recapture probabilities (noted P), defined as the probability that a shearwater alive at year t is caught during the breeding season of year t . The Cormack–Jolly–Seber model (CJS) is noted Φ_t, P_t , where both survival and capture probabilities varied freely over time, denoted t .

Two classical sources of lack of fit in capture–recapture studies arise from transient and trap dependence effects. The transient effect arises with birds that disperse from the study population in spite of breeding, or birds that breed in an inaccessible crevice nearby in future years (Tavecchia *et al.*, 2001). Trap dependence and especially trap happiness (a bird seen in year t is much more likely to be seen in year $t + 1$ than a bird not seen in year t) is common in seabird capture–recapture

data because most of the seabirds are extremely faithful to their breeding colony (Jenouvrier *et al.*, 2005). To detect transient and trap-dependent effects, goodness-of-fit (GOF) tests for the CJS model were computed for each location and sex (see Table A1) using the program U-Care (Choquet *et al.*, 2005). Overall, there were large discrepancies between study sites and sex. Trap happiness (denoted by m) is detected for males in Corsica and females in Crete, and the trap dependence models ($\Phi_t, P_{t \cdot m}$) fit the data ($P = 0.13$ and 0.85 , respectively). A transient effect is detected only for Selvagem birds for both sexes and is denoted by $a2$ for two classes of apparent 'age' (i.e. time elapsed since marking). The transient model ($\Phi_{t \cdot a2}, P_t$) fits the data ($P = 0.84$ and 0.23 for females and males, respectively).

The umbrella (i.e. most general) model is thus ($\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti $\Phi_{t \cdot s \cdot a2}$ Selvagem $P_{t \cdot \text{♂}}$ Corsica, ♀ Crete $P_{t \cdot s}$ Frioul, Malta, Tremiti, Selvagem $P_{t \cdot m}$ ♀ Corsica, ♂ Crete), and its construction is detailed in the Appendix (see also Gimenez *et al.*, 2003 for model development, and Frederiksen *et al.*, 2004 and Crespin *et al.*, 2006 for applications to other species). From the umbrella model, simpler models are fitted successively and Akaike's information criterion corrected for small sample size (AIC_c ; see Anderson & Burnham, 1999) is used for model comparison. The best model is the one with the lowest AIC_c [i.e. the most parsimonious model in terms of the number of parameters and data fit (model deviance)]. These analyses were run in the program M-SURGE (Choquet *et al.*, 2004). To enable identification of biological processes responsible for variation in survival rates, the total variance was decomposed into sampling variance and process variance (Gould & Nichols, 1998), and the process variance was estimated with program MARK (White & Burnham, 1999). To compare process variance among the populations, the process variance was calculated relative to the maximum possible variance (Morris & Doak, 2004).

The similarity of temporal variability in survival was calculated between all possible pairs among the six populations (Harris *et al.*, 2005; and Table A2). The tests of covariate effects are based on an analysis analogous to analysis of variance called ANODEV (Table A2). Under H_0 , the covariate did not explain any of the survival variance. To assess the effects of covariates, the amount of variation in survival accounted for by covariates (R^2) was estimated according to the model's deviance (Table A2; Gaillard *et al.*, 1997), or the process variance [calculated as $(\sigma^2 - \sigma_{\text{res}}^2)/\sigma^2$, where σ^2 refers to the total process variance and σ_{res}^2 to estimated residual variance when the effects of covariate are accounted for; see Loison *et al.*, 2002].

Table 1 Modeling (a) capture and (b) survival probabilities for Cory's shearwater

Question	Model name	k	Dev	ΔAIC_c
(a)				
Umbrella model	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti $\Phi_{t \cdot s \cdot a2}$ Selvagem $P_t \delta$ Corsica, φ Crete, $P_t \cdot s$ Frioul, Malta, Tremiti, Selvagem $P_t \cdot m \varphi$ Corsica, δ Crete	207	7197	33
1. Trap dependence effect?	$P_t \cdot s$ Corsica, Crete, Frioul, Malta, Tremiti, Selvagem	193	7247	55
2. Additive trap dependence effect?	$P_t \cdot s \delta$ Corsica, φ Crete, Frioul, Malta, Tremiti, Selvagem $P_{t+m} \varphi$ Corsica, δ Crete	197	7219	35
3. Additive sex effect?	P_{t+s} Frioul, Malta, Tremiti, Selvagem P_{t+s+m} Corsica, Crete	161	7261	5
4. Sex effect according to different study sites?	P_t Frioul, Malta, Tremiti, Selvagem P_{t+s+m} Corsica, Crete	157	7279	15
<i>For sake of simplicity, we did not show the test for each study site</i>	P_t Malta, Tremiti, Selvagem P_{t+s} Frioul P_{t+s+m} Corsica, Crete	158	7262	0
5. Additive time effect?	$P_{t+(Malta, Tremiti, Selvagem, +s Frioul, s+m Corsica, Crete)}$	123	7737	405
6. Time effect?	P_t Malta, Tremiti, Selvagem P_s Frioul P_{s+m} Corsica, Crete	120	7716	378
(b)				
Umbrella model	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti $\Phi_{a2 \cdot t \cdot s}$ Selvagem P_t Malta, Tremiti, Selvagem P_{t+s} Frioul P_{t+s+m} Corsica, Crete	158	7262	72
1. Transient effect?	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti, Selvagem	145	7302	86
2. Additive transient effect?	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti $\Phi_{(a2+t) \cdot s}$ Selvagem	148	7273	63
3. Additive sex effect?	Φ_{t+s} Corsica, Crete, Frioul, Malta, Tremiti Φ_{a2+t+s} Selvagem	109	7312	24
4. Sex effect according to different study sites?	Φ_t Corsica, Crete, Frioul, Malta, Tremiti Φ_{a2+t} Selvagem	98	7322	12
<i>For sake of simplicity, we did not show the test for each study site</i>	Φ_t Corsica, Frioul, Malta, Tremiti Φ_{t+s} Crete Φ_{a2+t} Selvagem	101	7315	11
5. Additive time effect?	$\Phi_{t+(Corsica, Frioul, Malta, Tremiti, s+Crete, a2+Selvagem)}$	68	7377	7
6. Time effect according to different study sites?	Φ_{t+} {1.(Corsica, Tremiti, a2 Selvagem); 2. (Crete φ , Frioul); 3.(Crete δ , Malta)}	64	7378	0
<i>All the possible combinations of study sites are not showed here for sake of simplicity</i>	Φ_t {1.(Corsica, Tremiti, a2 Selvagem), 2. (Crete φ , Frioul), 3. (Crete δ , Malta)}	57	7413	21

Akaike's information criterion corrected for small sample size (AIC_c) is used for model comparison, and for the identification of the best model (lowest AIC_c). ΔAIC_c is the difference of AIC between the specified model and the best one (i.e. $\Delta AIC_c = 0$ for the best model) in each table. k refers to the number of parameters estimated and Dev to the deviance of the model. The CJS model is $\Phi_t P_t$, with the survival probability (Φ) and capture probability (P) varying with time (t). An effect of sex on survival or capture rate is denoted by s , the letter m denotes apparent 'trap happiness' on recapture rates, and a transient effect on adult survival is denoted by $a2$ (see 'Material and methods' for more details).

Table 2 Effect of longitude and body size on adult survival variation of the six studied populations of Cory's Shearwater

Models	Dev	<i>k</i>	Slope	ICL	ICH	ANODEV <i>F</i> (1,11)	<i>P</i> -value	<i>R</i> ² σ Dev
Sex \times study sites	7431.1	65						
Longitude	7455.3	55	-0.0015	-0.023	-0.006	5.7	0.04	30–34
Body size	7465.8	55	0.0730	-0.027	0.173			
Constant	7467.9	54						

Dev is the deviance, *k* the number of parameters estimated, while IC refers to the 95% confidence intervals of the slope. To assess the effect of covariates, we determined whether the slope of the relationship between adult survival and the environmental variable was significant (i.e. does 0 belong to the confidence interval of the slope estimate?). If the slope is significant, we thus used the ANODEV to test for the covariate effect. The threshold *P*-value used for ANODEV was 0.05. We estimated the proportion of explained temporal variation in adult survival accounted by covariates (*R*²) based on the process variance (σ), and based on the deviance, respectively.

Results

Recapture rates

The most parsimonious model constrained detection probabilities to vary between years with additive trap happiness for males in Corsica and females in Crete, and with differences between sexes in the localities of Frioul, Corsica, and Crete (Table 1a). Recapture rates were highly divergent across study sites (Fig. 2a), and this is due to the differences in sampling schemes of the monitoring programs. For example, on Lavezzi capture–recapture efforts occurred during the prelaying stage when females visit their nests irregularly, whereas males visit them nearly every night. This favored the capture of males vs. females.

Adult survival

The mean annual adult survival rate of Cory's shearwater was 0.90 and the relative process variance (i.e. process variance taken relative to the maximum possible variance) is 0.0049. Mean annual adult survival ranges from 0.83 ± 0.0016 (mean \pm relative process variance) for both sexes in Malta to 0.95 ± 0.009 for females from Selvagem (Fig. 3a). There is evidence of a longitudinal gradient among the population (ANODEV, *P* = 0.04; Table 2, Fig. 3a), with 34% of the variation among population explained by a longitudinal gradient. There is no evidence of a body mass effect on adult survival (ANODEV, *P* = 0.43; Table 2), although there is a tendency for larger birds to have higher survival rates (Fig. 3b).

The most parsimonious model constrained adult survival to vary synchronously between localities, with differences between sexes in Crete and a transient effect in Selvagem (Table 1b). Adult survival probabilities were not dissimilar between the following groups: (1) both females and males from Selvagem, Corsica, Tremiti; (2) both females and males from Frioul and

females from Crete; and (3) both females and males from Malta and males from Crete (Fig. 2b). Adult survival probabilities varied from year to year between (1) 0.88 and 0.96, (2) 0.82 and 0.92, and (3) between 0.74 and 0.88. Lower survival rates occurred in 1990 and 1995; if these values are excluded, the relative process variance relative is reduced by 82% (0.09). The fraction of variability accounted for by the common patterns among possible pairs of localities ranges from 37% for Frioul/Crete to 92% for Tremiti/Malta, and is overall very high (average 71%) (Table 3). The temporal adult survival variations are affected by SOI (ANODEV, *P* < 0.0001; Table 4, Fig. 3c), but not by NAO (Table 4). The proportion of explained variation in survival by SOI was high (92% based on deviance and 62% based on the process variance).

Discussion

Our results showed that temporal variations in Cory's shearwater adult survival from six breeding populations were synchronized over a wide range of the species' distribution between 1989 and 1997. Adult survival varied between 0.88 and 0.96 for birds breeding in Selvagem, Corsica, and Tremiti Islands; 0.82 and 0.92 for females breeding in Crete and birds from Frioul Island; and between 0.74 and 0.88 for males breeding in Crete and birds from Malta.

Adult survival varied little from year to year, except during 1990 and 1995, where it decreased strongly. As expected for a long-lived species such as the Cory's shearwater, the interannual adult survival variations are small because of the effect of environmental canalization (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003). If the 1990 and 1995 lower adult survival years are removed, the process variance of adult survival drops by 82%. These results suggest that extreme events might be a likely factor affecting adult survival of Cory's shearwater.

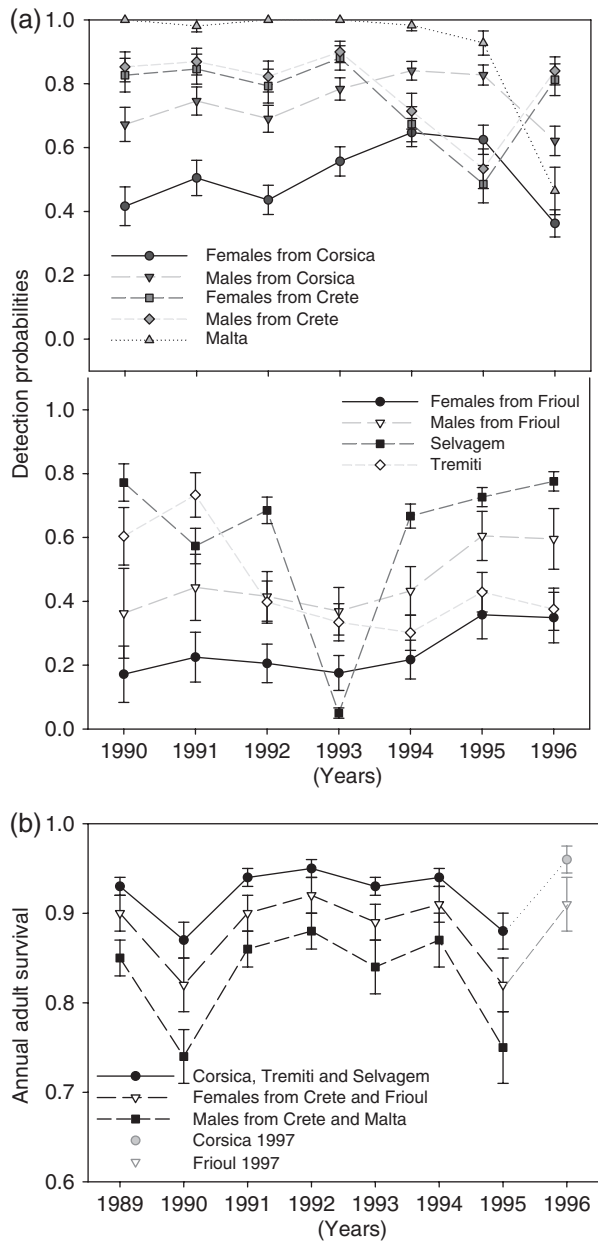


Fig. 2 (a) Capture probabilities and (b) survival rates according to study sites. Estimates \pm standard errors were computed from the best model $\Phi_{t+1}(\text{Corsica, Tremiti, } a_2 \text{ Selvagem})$; 2.(Crete ♀, Frioul); 3.(Crete ♂, Malta) P_t Malta, Tremiti, Selvagem P_{t+s} Frioul P_{t+s+m} Corsica, Crete. Because trap-dependent models have severe identifiability problems (Pradel, 1993), we showed the estimates of adult survival from Corsica and Frioul in 1996, computed by another analysis over the entire period of the study (unpublished results). The estimates \pm standard errors were computed from the best model $\Phi_t P_{t+s+m}$ and $\Phi_t P_{t+s}$ for Corsica between 1978 and 2004 and Frioul between 1981 and 2004, respectively. For the sake of visibility, we represented the variability in detection probabilities in two panels.

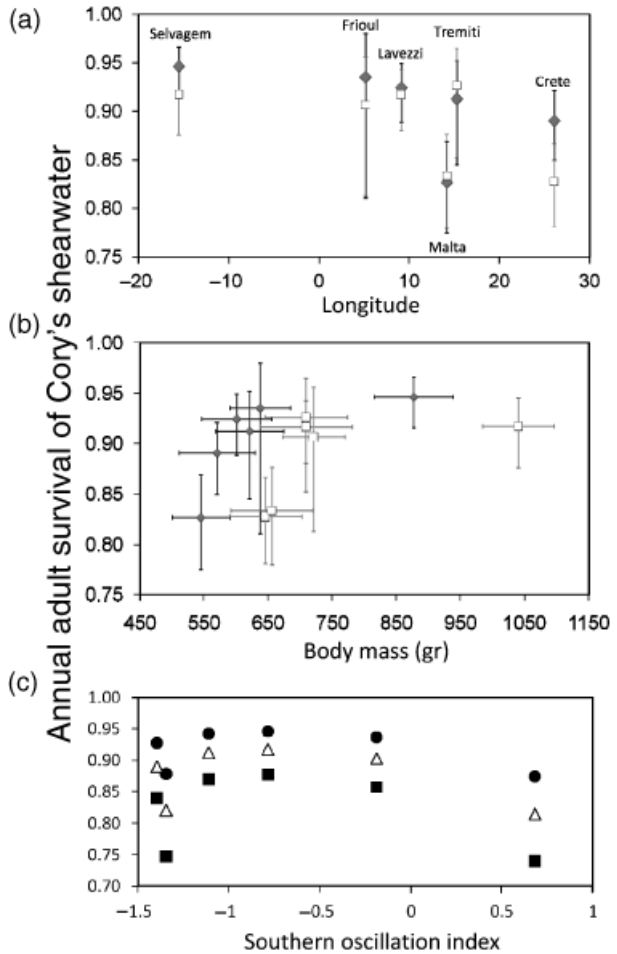


Fig. 3 Cory's shearwater mean adult survival rate for both sexes and across studies sites as a function of (a) longitude and (b) body mass. Gray diamonds represent females and black squares represent males. Estimates \pm standard errors are computed from the model $\Phi_{(\text{Crete, Corsica, Frioul, Malta, Tremiti, } a_2 \text{ Selvagem})} \cdot s$. (c) Temporal variations in Cory's shearwater adult survival rate between 1989 and 1997 as a function of the Southern Oscillation Index for the three groups (1) both females and males from Selvagem, Corsica, Tremiti (black circles), (2) both females and males from Frioul and females from Crete (triangles), and (3) both females and males from Malta and males from Crete (black squares). Estimates \pm standard errors are computed from the best model $\Phi_{t+1}(\text{Corsica, Tremiti, } a_2 \text{ Selvagem})$; 2.(Crete ♀, Frioul); 3.(Crete ♂, Malta).

Synchronicity explains on average 71% of adult temporal variations. Spatial synchronization of annual survival rates might be caused by the effect of environmental conditions during the nonbreeding season, when migratory seabirds originating from different breeding populations congregate in similar areas (Schaub *et al.*, 2005). Cory's shearwaters appeared to

migrate to a widespread range in the South Atlantic, with birds breeding in the Atlantic (Selvagem) wintering more westward than those breeding in the Mediterranean (Ristow *et al.*, 2000). The widespread distribution during winter over a vast oceanic range allows seabirds to leave an area with adverse weather or trophic conditions (Harris *et al.*, 2005), and extreme environmental events occurring at large spatial scale may be a likely factor affecting adult survival. Wrecks of large numbers of seabirds, including Cory's shearwaters, have been recorded related to autumn and northern-winter storms in the course of migration and wintering area of Cory's shearwater (Brichetti *et al.*, 2000).

Our results support the hypothesis that extreme events due to large-scale climate oscillations occurred during the nonbreeding season and influenced Cory's shearwater adult survival. The SOI appears to be an important source for the temporal variation of Cory's shearwater adult survival, whereas the NAO has no effect. The NAO affects the North Atlantic and Mediterranean climate where the breeding populations are located, whereas the effect of the SOI is expected only during the nonbreeding season when the birds migrate southward in the Atlantic. Adult survival is negatively affected by the SOI (positive SOI values indicated La Niña years), with at least 62% of the variation in survival explained by SOI fluctuations. During La Niña years, the greater number of Atlantic hurricanes and storms may cause a decrease in adult

survival for Cory's shearwater. Wrecks of pelagic seabirds following hurricanes and storms generally tend to be dominated by juvenile birds rather than adults. Therefore, the effect of storms during La Niña suggested here for adults will likely affect juvenile survival even more.

Our results showed that large-scale climate forces affect and synchronize the adult survival of wide-ranging migratory bird over its entire range. The consequences of this result in terms of population dynamics depend on complex demographic processes (e.g. fecundity, recruitment, immigration, density dependence, and so on) and require modeling the meta-population, which is beyond the scope of this study. However, we speculate that the spatial synchronization of annual survival variations may unlikely translate into the spatial synchronization of interannual fluctuations in populations. Indeed, for long-lived species, Saether & Bakke (2000) suggested that variation in fecundity and recruitment contributes more to the population fluctuations than variations in adult survival. Spatial synchronization of fecundity and recruitment variability is unlikely for seabirds because the potential factors affecting them (e.g. ocean productivity around the breeding site, habitat quality, predation, etc.) may differ significantly among geographically distinct populations. Nevertheless, the synchronized reduction in adult survival for all populations during extreme climate events may likely have a direct consequence on the meta-population, because long-lived species population growth rate is very sensitive to adult survival. Ultimately, it will result in higher species extinction risk, especially if extreme climate events become more frequent.

Our results also highlight that mean adult survival rates differed between populations and between sexes for birds breeding in Crete. A longitudinal gradient explains 34% of the variance observed among mean adult survival. Adult survival is higher for birds breeding in the Atlantic (mean \pm relative process variance: 0.95 ± 0.03 for females, 0.93 ± 0.04 for males in Selvagem) than in the eastern part (0.89 ± 0.03 for females, 0.83 ± 0.03 for males in Crete). Several

Table 3 Covariation among study sites time series from 1989 to 1997

	Selvagem	Frioul	Lavezzi	Malta	Tremiti	Crete
Selvagem	58	77	88	90	51	
Frioul		74	60	88	37	
Lavezzi			46	79	87	
Malta				92	51	
Tremiti					86	
Crete						

Fraction of variation explained by a common pattern between study sites time series (%).

Table 4 Effect of SOI and NAO on adult survival variation of the six studied populations of Cory's shearwater

Models	Deviance	<i>k</i>	Slope	ICL	ICH	ANODEV <i>F</i> (1,7)	<i>p</i> _{ANODEV}	<i>R</i> ² σ -deviance (%)
Time	7378.1	64						
SOI	7408.2	58	-0.22	-0.41	-0.04	78.7	<0.0001	62-92
NAO	7713.1	58	-0.09	-0.47	0.29			
Constant	7746.7	57						

See Table 3 for legend. The threshold *P*-value used for ANODEV is 0.05 and a Bonferroni correction for two tests is applied. SOI, Southern Oscillation Index; NAO, North Atlantic Oscillation.

nonexclusive factors potentially explain this observed longitudinal gradient, including oceanographic constraints around the breeding populations, body size, and human impacts.

Oceanographic productivity around the breeding populations decreases eastward. The eastern Mediterranean is a nutrient-poor region with low productivity (Caddy *et al.*, 1995). In the Western Mediterranean, productivity is enhanced by cooler water from large rivers and currents from Atlantic along North Africa coasts (Margalef, 1985; Caddy *et al.*, 1995). Between Morocco and Selvagem Islands in the Atlantic, productivity is enhanced by strong upwelling with colder and richer waters (Freudenthal *et al.*, 2002).

Previous studies showed a longitudinal gradient in body size, with larger birds in the Atlantic than in the eastern Mediterranean (Rabouam *et al.*, 1998). This is probably a result of the selective pressure in relation to the observed water productivity gradient. Our analysis does not support an effect of body mass on Cory's shearwater. However, body weight had been collected at random, and the random weight of an individual varies by 15% within days whereas the weight distribution of a population shows a much smaller standard deviation (Ristow & Wink, 1980). To study the influence of body size on adult survival, the quality of the data should be improved in future studies by taking weights only at the end of the prelaying period to minimize the variation in weight among individuals, or by using measurements of skeletal features of birds.

Harvesting of Cory's shearwater and incidental bycatch by longline fisheries may also influence adult survival, with contrasting effects between the Atlantic and Mediterranean. Sixty-six percent of the birds killed as incidental bycatch are mainly adult Cory's shearwaters around Columbretes Islands in the Western Mediterranean (Belda & Sánchez, 2001). Interaction with fisheries varies depending on location (Cooper *et al.*, 2003), but more information is needed to quantify the impact of longline fisheries on Cory's shearwater mortality. The practice of harvesting of birds has sharply declined among most Mediterranean populations since the 1970s, with the exception of the Sicily channel where birds are killed illegally by fishermen in Malta (Borg & Cachia-Zammit, 1998). Birds breeding in Malta showed the lowest adult survival (0.827 ± 0.03 for females, 0.833 ± 0.03 for males), highlighting the effects of human harvesting.

Conclusion

Despite uncertainties over causal mechanisms, these findings add to the body of evidence that large-scale climate variations could affect seabird adult survival

over large spatial scales. We argue here that for long-lived seabird species, adult survival is buffered against regular environmental variability. Extreme climate conditions, such as storms, significantly affect adult survival at large spatial scales during the nonbreeding period. Whatever the exact causes may be, the effects of large-scale climatic processes are dramatic for species with high adult survival and low fecundity, because even minimal reductions in survival have large effects on population trends. Moreover, we showed here that variation in adult survival was synchronized over the entire distribution of the Cory's shearwater, resulting in reduced persistence of meta-populations. The future of such long-lived seabird species has the potential to be dire under future global changes, especially because there are predictions of higher frequency extreme large-scale climatic events, such as El Niño/La Niña events.

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References

- Altwegg R, Roulin A, Kestenholtz M, Jenni L (2006) Demographic effects of extreme winter weather in the barn owl. *Oecologia*, **149**, 44–51.
- Anderson DR, Burnham KP (1999) General strategies for the analysis of ringing data. *Bird Study*, **46**, S261–S270.
- Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 2111–2116.
- Belda EJ, Sánchez A (2001) Seabird mortality in the Western Mediterranean: factors affecting bycatch and proposed mitigating measures. *Biological Conservation*, **98**, 357–363.
- Borg JJ, Cachia-Zammit R (1998) Monitoring Cory's shearwater *Calonectris diomedea* populations in a hostile environment. In: *Ecologie des oiseaux marins et gestion intégrée du littoral en Méditerranée* (eds Walmsley J, Goutner V, El Hili A, Sultana J) IV Symposium Méditerranée des Oiseaux Marins, Hammamet, Tunisia.

- Bretagnolle V, Lequette B (1990) Structural variation in the call of the Cory's shearwater. *Ethology*, **85**, 313–323.
- Brichetti P, Foschi UF, Boano G (2000) Does El Niño affect survival rate of Mediterranean populations of Cory's shearwater? *Waterbirds*, **23**, 147–154.
- Caddy JF, Refk R, Do-Chi T (1995) Productivity estimates for the Mediterranean: evidence of accelerating ecological change. *Ocean & Coastal Management*, **26**, 1–18.
- Camphuysen CJ, Van Der Meer J (2001) Pelagic distribution, moult and (sub-) specific status of Cory's shearwaters *Calonectris (d.) diomedea/borealis* wintering off southern Africa. *Marine Ornithology*, **29**, 89–96.
- Choquet R, Reboulet AM, Pradel R, Gimenez O, Lebreton JD (2004) M-SURGE: new software specifically designed for multistate capture–recapture models. *Animal Biodiversity and Conservation*, **27**, 207–215.
- Choquet R, Reboulet AM, Pradel R, Gimenez O, Lebreton JD (2005) *U-Care User's Guide, Version 22*. Montpellier (ftp://ftpcefnrsr/biom/Soft-CR/U-CARE). CEFE, Montpellier, France.
- Cooper J, Baccetti N, Belda EJ, Borg JJ, Oro D, Papaconstantinou C, Sanchez A (2003) Seabird mortality from longline fishing in the Mediterranean Sea and Macaronesian waters: a review and a way forward. *Scientia Marina*, **67**, 57–64.
- Crespin L, Harris MP, Lebreton JL, Wanless S (2006) Increased adult mortality and reduced breeding success with age in a population of common guillemot *Uria aalge* using marked birds of unknown age. *Journal of Avian Biology*, **37**, 273–282.
- Duffy DC (1990) Seabirds and the 1982–83 El Niño Southern Oscillation. In: *Global Ecological Consequences of the 1982–1983 El Niño Southern Oscillation* (ed. Glynn PW), pp. 395–415. Elsevier Oceanographic Series 52, Amsterdam, the Netherlands.
- Frederiksen M, Harris MP, Wanless S (2005) Inter-population variation in demographic parameters: a neglected subject? *Oikos*, **111**, 209–214.
- Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson L (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, **41**, 1129–1139.
- Freudenthal T, Meggers H, Henderiks J *et al.* Upwelling intensity and filament activity of Morocco during the last 250,000 years. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **49**, 3655–3674.
- Gaillard JM, Boutin JM, Delorme D, Van Laere G, Duncan P, Lebreton JD (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.
- Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.
- Gimenez O, Choquet R, Lebreton JD (2003) Parameter redundancy in multistate capture–recapture models. *Biometrical Journal*, **45**, 704–722.
- Gould WR, Nichols JD (1998) Estimation of temporal variability of survival in animal populations. *Ecology*, **79**, 2531–2538.
- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton M, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, **430**, 71–75.
- Harris MP, Anker-Nilssen T, McCleery RH, Erikstad KE, Shaw DN, Grosbois V (2005) Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. *Marine Ecology Progress Series*, **297**, 283–296.
- Hudson PJ (1985) Population parameters for the Atlantic alcidae. In: *The Atlantic Alcidae* (eds Nettleship DN, Birdhead TR), pp. 233–261. Academic Press, London.
- Jenouvrier S, Barbraud C, Weimerskirch H (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology*, **72**, 576–587.
- Jenouvrier S, Barbraud C, Weimerskirch H (2005) Long-term contrasted responses to climate of two Antarctic seabirds species. *Ecology*, **86**, 2889–2903.
- Jenouvrier S, Tavecchia G, Thibault J-C, Choquet R, Bretagnolle V (2008) Recruitment processes in long-lived species with delayed maturity: estimating key demographic parameters. *Oikos*, **117**, 620–628.
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lebreton JD, Clobert J (1990) Bird population dynamics, management and conservation: the role of mathematical modelling. In: *Bird Population Studies: Their Relevance to Conservation and Management* (eds Perrins CM, Lebreton JD, Hiron GJM), pp. 105–125. Oxford University Press, Oxford, UK.
- Loison A, Sæther BE, Jerstad K, Røstad OW (2002) Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics*, **29**, 289–304.
- Margalef R (1985) Environmental control of the mesoscale distribution of primary producers and its bearing to primary production in the western Mediterranean. In: *Mediterranean Marine Ecosystems* (eds Moraitou-Apostopoulou M, Kiortsi V), pp. 213–229. Plenum Press, New York.
- Morris WF, Doak DF (2004) Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *American Naturalist*, **163**, 579–590.
- Mougin JL, Jouanin C, Roux R (2000) Démographie du Puffin cendré *Calonectris diomedea de Selvagem Grande* (30°09'N, 15°52'W). *Revue d'Écologie*, **55**, 275–290.
- Ottersen G, Planque B, Belgrano A, Post E, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.
- Pradel R (1993) Flexibility in survival analysis from recapture data: handling trap-dependence. In: *Marked Individuals in the Study of Bird Populations* (eds Lebreton JD, North PM), pp. 29–37. Birkhäuser Verlag, Basel, Switzerland.
- Rabouam C, Bretagnolle V, Thibault J-C (1998) Geographic variation in the breeding biology of the Cory's shearwater: an effect of body size or environment? In: *Ecologie des oiseaux marins et gestion intégrée du littoral en Méditerranée*. 4^{ème} Symposium Méditerranéen des Oiseaux Marins, Hammamet, Tunisia.
- Ristow D, Berthold P, Hashmi D, Querner U (2000) Satellite tracking of Cory's shearwater migration. *Condor*, **102**, 696–699.

- Ristow D, Wink M (1980) Sexual dimorphism of Cory's shearwater. *II-Merill*, **21**, 9–12.
- Rolland V, Barbraud C, Weimerskirch W (2008) Combined effects of fisheries and climate on a migratory long-lived marine predator. *Journal of Applied Ecology*, **45**, 4–13.
- Royama T (1992) *Analytical Population Dynamics*. Chapman & Hall, London.
- Saether BE, Bakke O (2000) Avian life history variation and contribution of demographic trait to the population growth rate. *Ecology*, **81**, 642–653.
- Sandvik H, Erikstad K, Barrett R, Yoccoz G (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, **74**, 817–831.
- Sarà M (1993) Feeding habits of Cory's shearwater (*Calonectris diomedea*) in the Central Mediterranean Sea. In: *Status and Conservation of Seabirds* (eds Aguilar JS, Monbailliu X, Paterson AM), pp. 213–220. Proceedings of the 2nd Mediterranean Seabird Symposium MEDMARAVIS/SEO, Madrid, Spain.
- Schaub M, Wojciech K, Koppens U (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology*, **74**, 656–667.
- Stearns SC (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Stenseth NC, Ottersen G, Hurrell JW *et al.* (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B*, **270**, 2087–2096.
- Stenseth NC, Ottersen G, Hurrell JW, Belgrano A (2004) *Marine Ecosystems and Climate Variation: The North Atlantic: A Comparative Perspective*. Oxford University Press, Oxford, UK.
- Tavecchia G, Pradel R, Boy V, Johnson A, Cézilly F (2001) Sex- and age-related variation in survival probability and the cost of the first reproduction in breeding greater flamingos. *Ecology*, **82**, 165–174.
- Thibault JC, Rabouam C, Bretagnolle V (1997) *Calonectris diomedea* Cory's shearwater. *Birds of the Western Palearctic*, Update 1, 75–98.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–138.

Appendix A: Goodness of fit test and model

Goodness-of-fit tests

Table A1 Results of goodness-of-fit (GOF) tests of CJS model (Φ_t, P_t), for each location and sex

Location	Sex	Test												GOF test for the umbrella model with ...						Chosen model			
		3SR			3SM			2CT			2CL			TraP dePence			Transients				None (CJS model)		
		df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P		df	χ^2	P
CORSICA	♀	7	2.2	0.949	7	18.3	0.011	6	7.7	0.259	6	5.8	0.444	20	26.3	0.156	19	31.8	0.033	26	34.0	0.134	$\Phi_t P_t$
	♂	6	8.5	0.206	7	9.7	0.204	6	27.0	0.000	5	6.7	0.242	18	24.9	0.127	18	43.5	0.001	24	52.0	0.001	$\Phi_t P_{t-m}$
CRETE	♀	7	2.4	0.937	6	7.7	0.265	6	22.7	0.001	5	2.0	0.846	18	12.0	0.845	17	32.4	0.013	24	34.8	0.072	$\Phi_t P_{t-m}$
	♂	6	3.6	0.728	6	0.8	0.993	6	3.2	0.787	3	3.4	0.334	15	7.8	0.932	15	7.3	0.948	21	11.0	0.964	$\Phi_t P_t$
MALTA	♀	6	4.3	0.631	2	0.5	0.775							8	4.9	0.773	2	0.5	0.775	8	4.9	0.773	$\Phi_t P_t$
	♂	6	8.3	0.220	3	2.8	0.430	1	1.2	0.271				9	11.0	0.274	4	4.0	0.410	10	12.2	0.270	$\Phi_t P_t$
FRIOUL	♀	5	6.4	0.267				6	7.5	0.274	5	2.2	0.818	10	8.7	0.566	11	9.8	0.552	16	16.2	0.440	$\Phi_t P_t$
	♂	7	4.8	0.681	6	7.7	0.262	6	5.2	0.520	5	4.1	0.534	18	16.6	0.549	17	17.0	0.455	24	21.8	0.590	$\Phi_t P_t$
SELVAGE	♀	7	22.3	0.002	7	5.5	0.599	6	4.0	0.677	5	2.7	0.746	19	30.5	0.046	18	12.2	0.837	25	34.5	0.098	$\Phi_{a2-t} P_t$
	♂	6	17.5	0.008	6	10.8	0.096	6	4.8	0.564	5	5.3	0.379	17	33.6	0.009	17	20.9	0.230	23	38.4	0.023	$\Phi_{a2-t} P_t$
TREMITI	♀	5	2.5	0.783	5	6.2	0.284	6	7.1	0.310	6	3.0	0.809	16	11.7	0.764	17	16.4	0.498	22	18.8	0.656	$\Phi_t P_t$
	♂	6	7.9	0.243	5	6.8	0.233	6	3.1	0.801	5	7.9	0.161	16	22.7	0.122	16	17.8	0.335	22	25.8	0.262	$\Phi_t P_t$

When the specific tests for transients or trap-happiness were significant, we tested the GOF of the more general model (Φ_{t-a2}, P_t) or (Φ_t, P_{t-m}). For each study locality, we first assessed the fit of the most general model (Φ_{t-sr}, P_{t-s}) with both survival and recapture rate varying among years and sexes, using TEST2 and TEST3. TEST 2 examines the independence between year of last release and year of next recapture. TEST 3 checks the homogeneity of resighting histories at any release time (Burnham *et al.*, 1987). In cases when model (Φ_{t-sr}, P_{t-s}) did not fit the data, we used the sum of TEST 2 + TEST 3SM to assess the goodness of fit (GOF) of model that take into account 'transients' (Φ_{t-s-a2}, P_{t-s}) and the sum of TEST 3 + TEST 2CL to assess the goodness of fit of model that consider 'trap dependence' (Φ_{t-sr}, P_{t-s-m}) (see Pradel, 1993). Empty boxes refer to cases when there were not sufficient data to compute GOF test, and significant tests appear in bold.

Model development

Gimenez *et al.* (2003) showed that a model taking into account both the effects of trap dependence on detection probabilities and transience on survival probabilities could be written in a multi-state framework as:

$$\Phi_t = \begin{matrix} \text{Seen before} & \text{Seen at } t & \text{Not seen at } t \\ \begin{pmatrix} \Phi_{a2,t} P_t & \Phi_{a2,t} (1 - P_t) \\ \Phi_{a2,t} P_t^* & \Phi_{a2,t} (1 - P_t^*) \end{pmatrix} & & \end{matrix} \quad P_t = \begin{matrix} \text{Seen before} \\ \text{Not seen before} \end{matrix} \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

Where P_t and P_t^* are the capture probabilities at time t for an individual caught at the previous occasion or not, respectively; Φ_t is the survival probabilities between time t and $t + 1$. Trap happiness stands for $P_t > P_t^*$. To include transient effects, we took into account an age effect on survival, noted $a2$ with $\Phi_{a1 \cdot t} < \Phi_{a2 \cdot t}$. (Table A2)

Table A2 Summary of the calculations used to study the similarity of variability in temporal survival among the six populations and the effect of covariates on survival probabilities

Question of interest	Calculation	Notation of models (M) and parameters
similarity of temporal survival variation	$[\text{DEV}(M_p) - \text{DEV}(M_{p+t})] / [\text{DEV}(M_p) - \text{DEV}(M_{p \cdot t})]$	M_p : constant survival according to population, M_{p+t} : similar time variations between populations, $M_{p \cdot t}$: time effect for each population.
effects of body size and longitudinal gradient on adult survival	F -statistic of the ANODEV test: $[\text{DEV}(M) - \text{DEV}(M_c)] / [(\text{DEV}(M_c) - \text{DEV}(M_g)) / k - 1]$	M : constant survival, M_c : covariate, M_g : constant survival according to study sites and sex (g standing for 12 groups, 2 sex · 6 study sites), k : number of parameters of the survival vector (12 for 12 groups)
amount of variation in survival accounted for by covariates (R^2)	$[\text{DEV}(M_c) - \text{DEV}(M)] / [\text{DEV}(M_g) - \text{DEV}(M)]$	
effects of climatic oscillations on adult survival	F -statistic of the ANODEV test: $[\text{DEV}(M) - \text{DEV}(M_c)] / [(\text{DEV}(M_c) - \text{DEV}(M_t)) / k - 1]$	M : constant survival, M_c : covariate, M_t : time varying survival
amount of variation in survival accounted for by covariates (R^2)	$[\text{DEV}(M_c) - \text{DEV}(M)] / [\text{DEV}(M_t) - \text{DEV}(M)]$	k : number of parameters of the survival vector (8 for 8 years)

The calculations are based on the deviance (DEV) of specific models. The effects of covariates are tested with an analysis analogous to analysis of variance, called ANODEV. Under H_0 , the covariate does not explain any of the survival variance [$F \sim F(1, k-1)$].