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ARTICLE
Animal Ecology

Temporal and spatial heterogeneity in dispersal and demography of a long-lived philopatric seabird

Ana Payo-Payo[1] | **Andreu Rotger**[2,3] | **Virginia Picorelli**[4] |
Mariana Viñas Torres[5] | **Esteban Cardona**[6] | **Oliver Martínez**[6] |
Ana Sanz-Aguilar[3,7]

[1]Animal Ecology Lab, Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense Madrid, Madrid, Moncloa-Aravaca, Spain

[2]Interdisciplinary Ecology Group, Departament de Biologia, Universitat de les Illes Balears, Palma de Mallorca, Spain

[3]Animal Demography and Ecology Unit, IMEDEA (CSIC-UIB), Esporles, Spain

[4]Servei de Planificació del Medi Natural, Conselleria de Medi Ambient i Territori, Govern de les Illes Balears, Palma, Spain

[5]Institut Balear de la Natura IBANAT, Conselleria de Medi Ambient i Territori, Govern de les Illes Balears, Palma, Spain

[6]Servei d'Agents de Medi Ambient, Conselleria de Medi Ambient i Territori, Govern de les Illes Balears, Palma, Spain

[7]Applied Zoology and Animal Conservation Group, University of Balearic Islands, Palma, Spain

Correspondence
Andreu Rotger
Email: andreu.rotger@uib.cat

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Abstract

Individuals make habitat selection decisions at different moments of their life and in heterogeneous habitats. Understanding the links between environmental changes and demographic patterns during the individuals' life is therefore critical to predict long-term eco-evolutionary dynamics and species persistence. However, fitness and persistence consequences of habitat selection are seldom addressed in demographic studies. We used long-term capture–recapture data of Mediterranean Storm Petrels to investigate how habitat-selection decisions are made at different spatial (i.e., among and within breeding zones) and temporal (i.e., natal and breeding fidelity) scales in a colony characterized by significant variation in habitat quality due to contrasting parasite infestation levels. Specifically, we evaluate whether birds hatched in and/or breeding at different zones experience different (1) fitness components (i.e., breeding success and survival) and (2) fidelity (i.e., natal and breeding fidelity). In addition, we (3) explore the causes, environmental cues, and consequences of nest fidelity versus dispersal. Finally, we project (4) how these differences influence population dynamics and persistence (i.e., population growth rate). Our findings reveal that habitat selection decisions have synergistic fitness consequences on multiple temporal and spatial scales considered. Specifically, breeders in the lower quality habitat zone (i.e., high tick infestation) exhibited

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Ana Payo-Payo and Andreu Rotger contributed equally to the work reported here.

reduced breeding success, local survival, and nest fidelity, but remained within their zone. Breeding success of individuals exhibiting nest dispersal marginally increased. Moreover, natal fidelity was lowest at the zone where fitness was highest. Overall, population growth rate at the colony suggests an annual population decline between 6% and 10%. Individuals seem to base their dispersal decision, but not their habitat selection choices on public information. As a result, birds do not experience increased fitness, indicating the potential presence of an evolutionary trap. Understanding the interplay between synergistic and opposing habitat choices is central to understanding species eco-evolutionary dynamics. Further, our results highlight exciting avenues for future research, when aiming to understand the complex and fundamental roles played by heterogeneity in habitat quality in species demography and eco-evolutionary dynamics, with significant implications for species management and conservation strategies.

KEYWORDS
dispersal, evolutionary trap, reproduction, storm petrel, survival, ticks

INTRODUCTION

The environment is structured across different spatial and temporal scales (Orians & Wittenberger, 1991). Likewise, individuals inhabiting an environment are influenced by processes operating at multiple hierarchical levels and at different spatial and/or temporal scales within each level (Ray & Hastings, 1996). These processes generate heterogeneity in food resources, predators, or parasites (Monticelli et al., 2008; Oro et al., 2004; Wanless et al., 2007). Individuals should be able to perceive and respond to such variations (McGarigal et al., 2016), resulting in heterogeneity in vital rates that directly impact population dynamics and, subsequently, population persistence (Brunner et al., 2017; Buderman et al., 2023; Herfindal et al., 2014). Processes operating at different scales are likely to have effects of varying magnitudes and/or directions on demographic rates; for instance, climate change can exacerbate the spread and impact of pathogens (Mora et al., 2022). To detect such effects, it is essential to correctly define the extent and the size of the units (i.e., resolution/grain) used in demographic data analysis (Lu & Walter, 2023). However, such information is seldom included in analysis despite often being available (Gaillard et al., 2010).

Individuals can respond to structured environmental heterogeneity through habitat selection and dispersal (Bowler & Benton, 2005; Oro et al., 1999). It is well known that dispersal deeply affects individual fitness, population dynamics and persistence. Dispersal—and its alternative, fidelity—is a multistep decision process: Individuals must first decide between dispersing and remaining at their natal area, and then those dispersing must decide where to settle. Theory predicts that individuals assess risks (e.g., predation, competition, and parasites) and engage (or not) with dispersal strategies that maximize successful breeding or survival (Luna et al., 2020; Morinay et al., 2024). These decisions require reliable information to reduce uncertainty about the alternatives. However, it is increasingly clear that habitat selection patterns might vary considerably across spatial and temporal scales (McGarigal et al., 2016).

Seabirds are an ideal model group for understanding synergistic and opposing effects of heterogeneity in the scale of habitat selection on population dynamics and persistence of spatially structured populations (Acker et al., 2021). This is because seabirds are long-lived, and although they engage in large-scale movements during migration, foraging and prospecting, they are highly philopatric at both the nest and colony scales, which allows for potential fitness consequences of heterogeneity in habitat selection to amplify over time (Schreiber & Burger, 2001). In particular, the Mediterranean Storm Petrel (*Hydrobates pelagicus melitensis*) is a small, pelagic seabird that nests in caves, crevices, and burrows on isolated islands and cliffs free of mammalian predators throughout the Mediterranean region. They can breed in dense colonies and exhibit high natal and breeding site fidelity (Bonadonna & Sanz-Aguilar, 2012). One of the densest known colonies of Mediterranean Storm Petrels is in Cap d'Es Migdia cave located on the islet of Espartar (Ibiza, Spain), where dense breeding conditions favor the local maintenance of parasites, particularly ticks (*Ornithodoros maritimus*), and associated pathogens (Furness & Monaghan, 1987; McCoy et al., 2016). Previous research suggests that within the same colony, there is heterogeneity in breeding habitat quality due to differential tick infestation levels (Sanz-Aguilar et al., 2020). As a result, in the zone with high ectoparasite infestation (i.e., the inner chambers) nestlings have significantly lower body condition and higher mortality probabilities than at the zone with low ectoparasite infestation (Sanz-Aguilar et al., 2020). However, whether these differences are consistent across time and their consequences on other fitness components (i.e., survival), fidelity, and subsequent population dynamics remains poorly understood (Gaillard et al., 2010).

Our goal was to quantify the effects of sources of heterogeneity in habitat selection on population dynamics of this spatially structured population. Specifically, we addressed the following questions: whether birds hatched in and/or breeding at zones with different habitat quality (i.e., differential parasite infestation levels) present different (1) fitness components (i.e., breeding success and survival) and (2) fidelity (i.e., nest fidelity and natal and breeding zone fidelity). Additionally, (3) we assess whether the estimated vital rates (i.e., reproduction, apparent survival and dispersal) influence population dynamics and persistence (i.e., population growth rate). To achieve our objectives, we combine 9 years of individual monitoring data with generalized linear mixed models (GLMMs, Bolker et al., 2009) and multi-event capture–mark–recapture models (ME-CMRM; Pradel, 2005) that account for unobservable and uncertain states, to estimate vital rates and parameterize a spatially and demographically structured population matrix model (Caswell, 2001; Morris & Doak, 2002).

MATERIALS AND METHODS

Data collection

Species and study site

The Mediterranean Storm Petrel is one of the smallest seabirds of the order Procellariiformes (average body mass, 28 g; Warham, 1990). Mediterranean Storm Petrels lay a single egg directly on the floor that is incubated by both partners for 40 days (Minguez, 1994). The earliest clutches are laid in the second half of April and the last eggs are laid in the first week of July. Chick rearing lasts about 63–70 days and most fledglings leave colonies in August (Minguez, 1994). Mediterranean Storm Petrels can breed in their first year, but this behavior is unusual, typically recruiting from 3 years old onwards, many in the vicinity of their natal nest (Bonadonna & Sanz-Aguilar, 2012; Sanz-Aguilar, Massa, et al., 2009). Once they recruit into the breeding population, petrels are highly philopatric and return to breed in the same nest year after year with average nest fidelity of 0.96 (Dell'Ariccia et al., 2015; Sanz-Aguilar, Massa, et al., 2009). During their first breeding attempt, inexperienced breeders typically show lower breeding success (Hernández et al., 2017) and exhibit a lower future survival probability compared to experienced breeders (EBs) (Sanz-Aguilar et al., 2008). This study was conducted on Espartar Island, a 20.5-ha island located within the Es Vedrà, Es Vedranell i els illots de Ponent Natural Reserve in the Balearic Islands, Spain (38° 57′ 31″ N, 1° 11′ 44″ E, Figure 1). Mediterranean Storm Petrels breed all around the island at low densities but concentrate at high densities in natural caves. The study site was the Cap d'Es Migdia cave, where around 250–300 Mediterranean Storm Petrel pairs breed annually (Sanz-Aguilar et al., 2020). The presence of ticks (*O. maritimus*) in this cave has been previously linked to both lethal and sub-lethal effects on Mediterranean Storm Petrels (Sanz-Aguilar et al., 2020). The cave has two accessible areas with distinct characteristics that result in different tick infestation levels (see fig. 1 in Sanz-Aguilar et al., 2020). The entrance of the cave is a wide and illuminated area where nests are in small cavities and rock debris and presents lower tick infestation. The inner chambers are narrow, dark, and humid; with nests located in small cavities, rock debris and dusty soil and tick infestation is much higher (Sanz-Aguilar et al., 2020). In both areas, Mediterranean Storm Petrels nest on the ground and most visible nests are accessible to researchers, that is, adults can be captured by hand in 78% of nests found in the entrance and in 86% of nests found in the inner chambers.

Colony monitoring

From 2014 to 2022, fortnightly during the breeding season (May–September), we monitored occupation and breeding success in all accessible nests at the entrance and inner chambers of the cave. During the study period, 364 places where storm petrels laid their eggs have been identified in the cave: 112 in the entrance (*e*) and 252 in the inner chambers (*c*). Annual occupation of these known nesting sites during the study period has been always under 65% in both areas, as the maximum number of breeding pairs recorded in the entrance has been 73 and 161 in the inner chambers. We assume that surveyed nests are representative of the colony since birds'

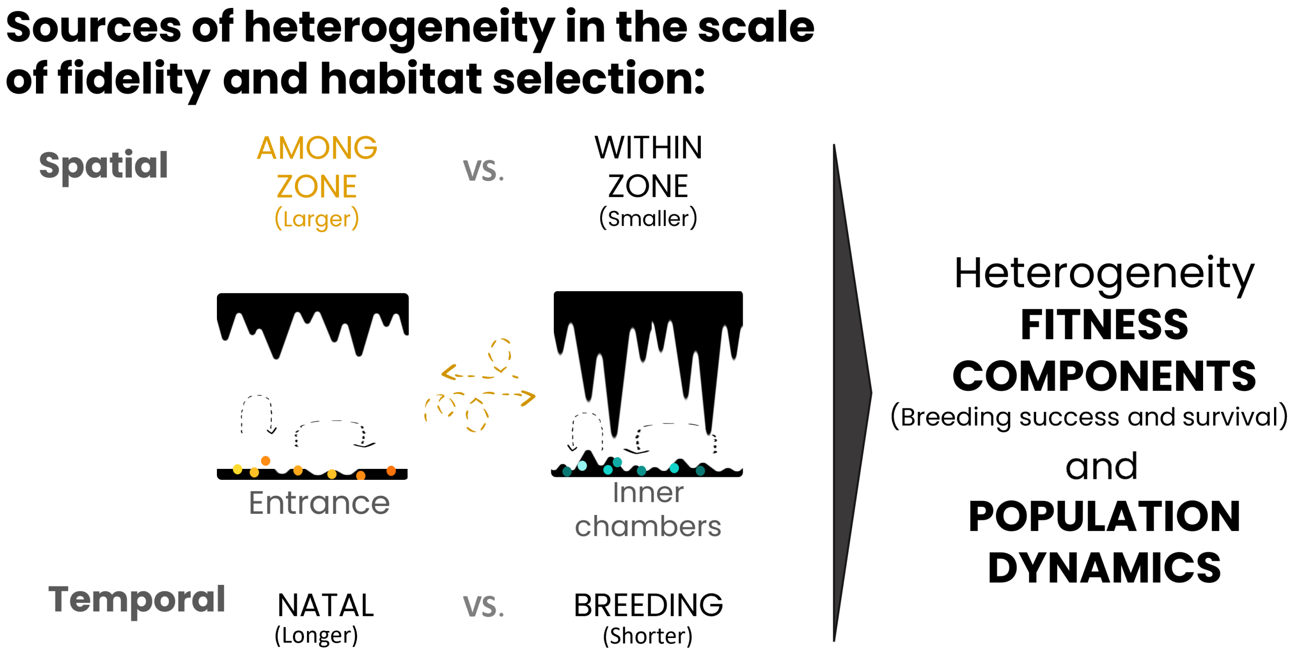

FIGURE 1 Conceptual framework highlighting considered sources of heterogeneity and demographic structure in habitat selection: spatial (i.e., among vs. within zone) and temporal (i.e., natal vs. breeding).

nest on the ground and most nests are both accessible and monitored.

Additionally, we annually captured and marked nestlings and breeding adults and recaptured previously marked birds. We marked a total of 482 nestlings ($N_E = 203$ and $N_C = 279$) and 679 breeding adults ($N_E = 197$ and $N_C = 482$) using unique alphanumeric metal rings. A total of 31 individuals marked as nestlings ($N_E = 16$ and $N_C = 15$) recruited in the breeding population ($N_E = 10$ and $N_C = 21$), total captures and recaptures of breeding adults were 1503 ($N_E = 489$ and $N_C = 1014$). Finally, during the years 2018, 2019, and 2020, we counted the number of tick larvae attached to the skin of storm petrel nestlings both in the entrance and in the inner chambers (Sanz-Aguilar et al., 2020). This study complies with the current European and Spanish laws regulating scientific research on animals. Permits were given by the Reserves Naturals D'es Vedrà, Es Vedranell I Els Illots De Ponent.

Estimation of infestation by ticks and vital rates

Tick infestation

We evaluated the differences in the number of ticks attached to the skin of storm petrel nestlings sampled at different ages by zone (i.e., *E*, entrance vs. *C*, inner chambers) by means of GLMMs (Bolker et al., 2009) with a Poisson error distribution and a log link function. All models included chick id, year, and decimal logarithm of nestling age as random factors to control for additional sources of variation as suggested in Sanz-Aguilar et al. (2020).

Nestling survival

We evaluated the differences in the nestling fate at the end of the breeding season (i.e., dead vs. alive) by zone and maximum observed number of ticks at any time during the nestling period by means of GLMMs (Bolker et al., 2009) with a binomial link function. All models included year random factors to control for additional sources of variation as suggested in Sanz-Aguilar et al. (2020).

Breeding success

We tested whether breeding experience (i.e., FTB, first-time breeder vs. EB) and zone (i.e., *E*, entrance vs. *C*, inner chambers) influenced breeding success by means of GLMMs, (Bolker et al., 2009) with a binomial link function. Breeding success was 1 when the nestling fledged and 0 when the egg did not hatch, or the nestling died. We use first-time observed breeding attempts as a proxy of experience by categorizing the first-time captured individuals as potential inexperienced breeders. To reduce confounding effects related to monitoring, we removed the data from 2014, as this first year all individuals were categorized as first-time observed breeders. Data from 2015 onwards were maintained in the analyses, although we acknowledge that we certainly categorized as inexperienced breeders some experienced animals, but not the opposite, that is, the effect of first-time breeding is very conservative. This approximation has been proved to be useful to study storm petrel demography (Sanz-Aguilar et al., 2008). We account for individual and year variability by including individual ID and year as random factors in all models. We also attempted running models including pair identity as a random factor, but models did not converge.

Nest fidelity

We evaluated potential differences in nest fidelity of birds breeding in different zones (i.e., entrance vs. inner chambers) by identifying the nest where each animal was captured during the study period. Subsequently, for those birds that were captured as breeders more than once, we calculated the mean observed number of different nests used by individuals controlling by the number of captures. In addition, we estimated the probability of nest change by area using GLMMs (Bolker et al., 2009) with a binomial link function.

Causes, sources of information, and consequences of nest dispersal

First, we evaluated the potential causes of nest dispersal by means of GLMMs (Bolker et al., 2009) by comparing the breeding success of the nests where individuals moved and stayed at time t (i.e., before anyone moved). Then, we evaluated the sources of information during nest dispersal by means of GLMMs (Bolker et al., 2009) by comparing the breeding success of the nests where individuals moved, before and after they moved (i.e., environmental cues /cause). This means that if a bird bred at nest A at time t and moved to nest B at time $t+1$, we compared the breeding success of nest A at time t (i.e., own breeding success) and breeding success of nest B at time t (i.e., environmental cue on breeding success). Finally, we evaluated the consequences of dispersal by comparing the breeding success of the birds that moved and remained at the same nest at consecutive time steps (t_0 and t_1) (i.e., fitness consequence of dispersal vs. nest site fidelity). Both sets of models included individual ID as a random factor and used a binomial link function.

Tick infestation, nestling survival, breeding success, nest fidelity, and drivers and consequences of nest dispersal models were all implemented in R software (R Core Team, 2013) using the *glmmTMB* package (Brooks et al., 2017).

Recruitment, natal, and breeding fidelity between zones and apparent survival

We used capture–recapture data of birds marked as nestlings and breeding adults to build individual encounter histories. Data were coded regarding the age (nestling vs. breeding adult) and the area in which the bird was captured (entrance vs. inner chambers). First, we checked our data for sources of heterogeneity in survival and/or recapture by goodness-of-fit tests (GOF; Appendix S1: Table S1). Since specific multievent GOF does not exist, we calculated the GOF of the Jolly Movement model (JMV) using U-CARE 3.3 (Choquet et al., 2009; Pradel et al., 2005). Then, we used multievent capture–recapture models to estimate recruitment, natal fidelity, breeding fidelity, survival, and recapture probabilities considering potential differences between zones and a potential effect of breeding experience on apparent survival (Pradel, 2005; Sanz-Aguilar et al., 2008). Here, due to imperfect detection, animals cannot be assigned to a first-time breeding state with certainty, but multievent models are specifically designed to deal with uncertainty in state assignment (Pradel, 2005). Consequently, our model based on five mutually exclusive events (nestlings and breeders captured or recaptured at the entrance and the inner chambers and not observed birds, see Appendix S2: Table S1) considered additional biological states to account for unobservable animals (i.e., non-breeders born at the entrance and inner chambers) and animals differing in breeding experience (FTB and EBs breeding at the different zones of the cave). In total, we considered 9 different states (Appendix S2: Table S1).

Multievent models consider three different types of parameters that model the initial state probabilities, the among-states transition probabilities (survival, recruitment, and fidelity) and the event probabilities conditional on individual state. The number of nestlings and breeding adults tagged varied annually depending on field effort and breeding success; therefore, we allowed initial state probability to vary with time and states for all models. We performed a 5-step model selection procedure. We first tested for temporal and zone effects on recapture probabilities. We then tested the effect of age in recruitment probability. For recruitment, based on previous evidence in other Mediterranean colonies (Sanz-Aguilar, Massa, et al., 2009), we allowed this parameter to vary from age 1 to age 7, and fixed recruitment to one (i.e., full recruitment) in the last age class. In birds, natal fidelity is typically lower than breeding fidelity, in terms of both distance and probability (Greenwood & Harvey, 1982). Therefore, we consider potential differences between natal and breeding fidelity, and test for differences between zones. If Mediterranean Storm Petrels use conspecific productivity as a proxy of site quality (Greenwood & Harvey, 1982; Pärt & Doligez, 2003), we expected higher natal fidelity of birds born at the entrance. On the other hand, given that nestling mortality is particularly high at the inner caves, we expect a lower breeding fidelity in this zone and a higher probability to move towards the entrance. Finally, once we selected the best model structure for recapture, recruitment, and fidelity, we evaluated the effect of the zone on apparent survival probabilities of non-breeders, FTBs, and EBs. Differences in apparent survival among non-breeders born at the entrance or the inner chambers could appear if nestlings born at the inner chambers fledged with poorer body condition or with higher endoparasite load potentially transmitted by ticks (Bush & Clayton, 2018; Gauthier-Clerc et al., 1998; Sanz-Aguilar et al., 2020). Differences in apparent survival between breeders at the two zones could appear due to lethal effects of ticks or associated infectious agents and/or to permanent dispersal out of the study area (Chambert et al., 2012; Gauthier-Clerc et al., 1998; Khan et al., 2019). All capture– recapture models were run in E-Surge software and model syntax is available in Appendix S3: Table S1.

Model selection

Model selection was based on Akaike's information criterion (AIC) in GLMM analyses and on second-order AIC adjusted for small sample sizes for capture–recapture analyses ($\mathrm{QAIC_c}$, Burnham & Anderson, 2002). We considered the model with lowest AIC as the best model, and those within two ΔAIC (the difference in AIC values) to be statistically equivalent (Burnham & Anderson, 2002). When two or more models were within 2 ΔAIC points, the Akaike's weight (w_i) was calculated as an index of relative model plausibility and used to obtain model-averaged estimates.

Observed and projected population dynamics

Observed population dynamics

We used data on nest occupation in areas consistently monitored in both the entrance and the inner chambers of the cave over the years to calculate the annual observed breeding population growth rates (N_{t+1}/N_t, where N is occupied nests and t is time). We discarded data from 2014 as during this first year of monitoring, we suspect that some occupied nests remained undetected and data are not comparable.

Projected population dynamics

We used a female-based post breeding census, age-stage-structured matrix model to estimate the expected dynamics of the population. We considered 20 stages in each site (k): 1 nestling (Nestling), 6 Non-Breeder stages differing in their age ($a\mathrm{NB}_k$ a ϵ [1–6]), 7 FTB stages differing in their age ($a\mathrm{FTB}_k$ a ϵ [1–7]), and 6 EB stages differing in their age ($a\mathrm{EB}k$ a ϵ [2–≥7]). This age-stage structure can be expressed in the form of a population projection matrix $\boldsymbol{A}$, that allows dispersal between zones:

		Entrance	Inner chambers
$\boldsymbol{A}$	Entrance	$\boldsymbol{A_{ee}}$	$\boldsymbol{A_{ce}}$
	Inner chambers	$\boldsymbol{A_{ec}}$	$\boldsymbol{A_{cc}}$

The projection matrix ($\boldsymbol{A}$) has sub-matrices $\boldsymbol{A_{od}}$, where "*o*" refers to the original (from) zone and "*d*" refers to the destination (to) zone. For example, $\boldsymbol{A_{ec}}$ is the projection matrix for the population that was in the entrance and moved to the inner chambers. As the full $\boldsymbol{A}$ and $\boldsymbol{A_{od}}$ matrices are cumbersome, they are presented in Appendix S4. We parameterized the projection matrix using the estimated demographic parameters (see above). Their variance was incorporated in the model by randomly selecting parameter values from a beta-distribution (Morris & Doak, 2002). We calculated the mean stochastic population growth rate λ and their SE running 10,000 stochastic population model simulations. To evaluate the role of between-zones dispersal on population dynamics, we also parameterized the projection matrix and calculated the expected population growth rate for a scenario where natal and breeding fidelity were 1 across areas.

RESULTS

Tick infestation and vital rate estimates

Ticks by zone

The number of ticks attached to nestlings in the entrance ($N_E = 0.07$; 95% CI: 0.02–0.22) was 83.31% lower than in the inner chambers ($N_c = 0.42$; 95% CI: 0.15–1.21) see Appendix S6: Table S1 (M_1, $\beta_E = -1.79$; 95% CI: −1.09 to −2.48) and Figure 2A.

Nestling survival

We found a negative relationship between nestling survival and the maximum number of ticks see Appendix S6: Table S2 ($\beta_{\text{Max\_ticks}} = -0.07$; 95% CI: −0.12 to −0.02). Accordingly, nestling survival was 2.43% lower in the inner chambers (see Appendix S6: Table S2; M_3, $\beta_C = -1.74$; 95% CI: −3.32 to −0.17, and Figure 2B).

Breeding success

We found an effect of zone (see Figure 2C and Appendix S6: Table S3; M_3, $\beta_C = -1.05$; 95% CI: −1.33 to −0.75) and experience on breeding success ($\beta_{EB} = 0.46$; 95% CI: 0.19–0.71). EBs showed 20% higher breeding success than FTBs, and individuals breeding in the entrance (*E*) experienced 86% higher breeding success than those breeding in the inner chambers (*C*) ($BS_{FTB,E} = 0.54$; 95% CI: 0.46–0.62, $BS_{FTB,C} = 0.29$; 95% CI: 0.24–0.36, $BS_{EB,E} = 0.65$; 95% CI: 0.58–0.72, $BS_{EB,C} = 0.40$; 95% CI: 0.33–0.46).

Nest fidelity, causes, sources of information, and consequences of nest dispersal

Raw data from 777 recaptures indicate that birds breeding in the inner chambers changed their nest more frequently than breeders in the entrance (Figure 2D; Appendix S5: Tables S1, Appendix S6: Table S4). Accordingly, model selection supported that the probability of nest fidelity within the same area was significantly

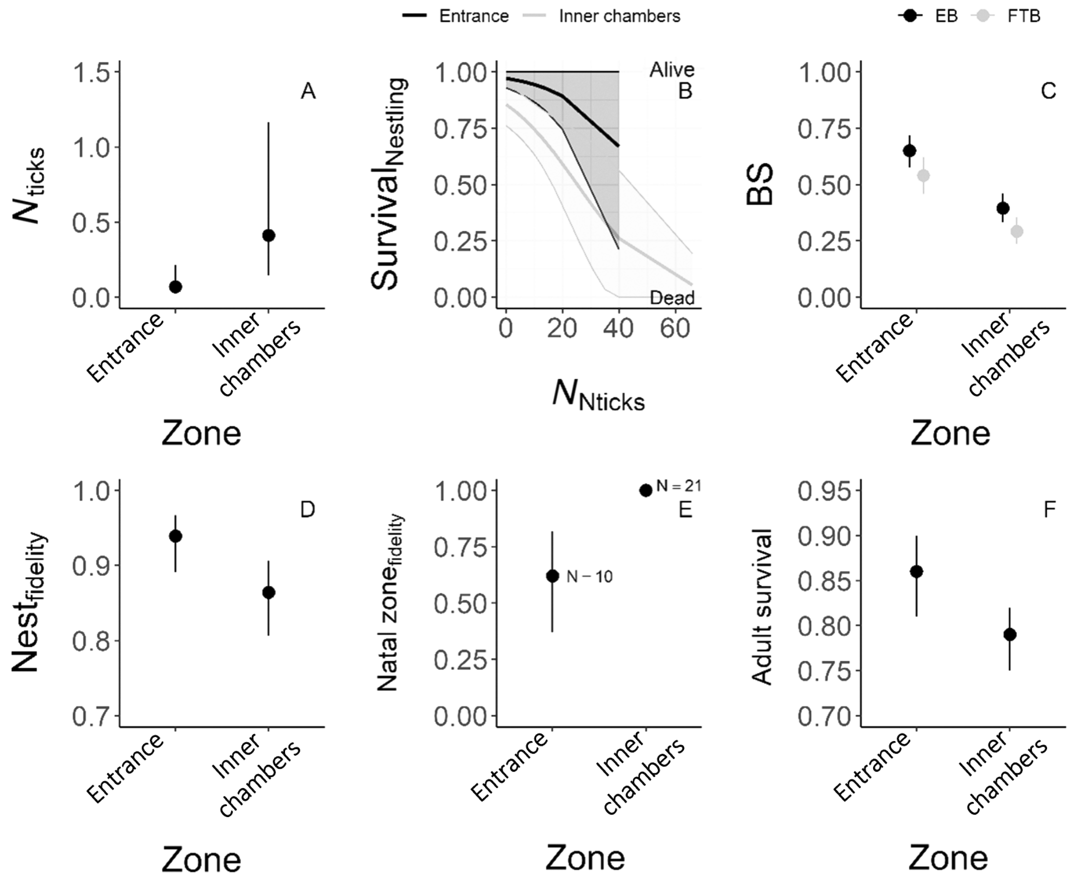

FIGURE 2 Differences in tick load and demographic parameters of Mediterranean Storm Petrels at the two zones (i.e., entrance vs. inner chambers) of Cap des Migdia colony at Espartar Island from 2014 to 2022. (A) Predicted number of ticks attached to nestlings (M_3, Appendix S6: Table S1). (B) Predicted survival of chicks assuming by maximum number of ticks (M_3, Appendix S6: Table S2). (C) Predicted breeding success (M_3–M_4, Appendix S6: Table S3), (D) Predicted nest fidelity (M_1, Appendix S6: Table S4). (E) Probability of natal zone fidelity (M_{12}, Appendix S6: Table S5). (F) Apparent adult survival probability (M_{12}, Appendix S6: Table S8). In panels (A) and (C–F) points and in panel (B) lines show predicted means and bars and the shaded area, respectively, show 95% CIs.

higher at the entrance (0.94; 95% CI: 0.89–0.97) than at the inner chambers (0.86; 95% CI: 0.80–0.91) ($\beta_E = 0.89$; 95% CI: 0.87–1.47; Appendix S6: Table S4). We found that breeding success was lower for individuals that subsequently changed nests than for individuals that remained in the same nest both in the inner chambers ($BS_C = 0.27$; 95% CI: 0.17–0.40 birds before changing nest vs. $BS_C = 0.41$; 95% CI: 0.34–0.48 before repeating nest) and at the entrance ($B_E = 0.56$; 95% CI: 0.41–0.70 before changing nest vs. $BS_E = 0.70$; 95% CI: 0.62–0.78 before repeating nest; future change $\beta = -0.63$; 95% CI: −0.06 to −1.19, Appendix S6: Table S5, M_3). Individuals did not disperse to more successful nests ($\beta_{\text{nest}} = -0.25$; 95% CI: −1.11 to −0.60, M_1–M_3, Appendix S6: Table S6) and dispersing did not improve their future probabilities of breeding successfully, M_1, Appendix S6: Table S7.

Natal, breeding fidelity, and apparent survival

Multievent capture–recapture models clearly supported differences in natal fidelity between zones while models including differences or equal breeding fidelity were similar in terms of $QAIC_c$ (Appendix S6: Table S8). A total of 31 known age birds recruited at the colony: 15 were born and recruited at the inner chambers; 10 were born and recruited at the entrance; and 6 were born at the entrance and recruited at the inner chambers. Natal fidelity in the entrance was estimated at 0.62 (95% CI: 0.37–0.82), while natal fidelity in the inner chambers was ~1 (Figure 2E; Appendix S7: Table S1). Regarding breeding fidelity, only 5 birds were observed changing their breeding zone (2 from the entrance to the inner chambers, 2 from the inner chambers to the entrance and back again to the inner chambers, and 1 bird from the inner chambers to the entrance) so this parameter in both zones was estimated at ~1 (Figure 2E; Appendix S7: Tables S1). Models considering differences in survival between juveniles, FTBs, and EBs were robustly supported in terms of $QAIC_c$, but differences in survival between zones were only clearly supported for EBs (Appendix S7: Table S1, Appendix S8: Figure S1). Model-averaged estimates of survival showed much lower in survival of FTBs compared with juveniles and non-breeders and EBs (Appendix S7: Table S1, Appendix S8: Figure S1). Juvenile and non-breeder survival was similar across zones, with values of 0.75 (95% CI: 0.66–0.83) in the entrance and 0.74 (95% CI: 0.65–0.81) in the inner chambers. Likewise, FTB survival was similar across zones with values of 0.51 (95% CI: 0.34–0.69) in the entrance and 0.49 (95% CI: 0.34–0.63) in the inner chambers (Appendix S7: Table S1, Appendix S8: Figure S1). EBs' survival was different across zones and much higher in the entrance with values of 0.86 (95% CI: 0.81–0.90) than in the inner chambers where survival was 0.79 (95% CI: 0.75–0.82; Figure 2F; Appendix S7: Table S7, Appendix S8: Figure S8). Full model results including initial state, recruitment, and recapture probabilities are available in Appendix S9: Table S1.

Observed and projected population dynamics

Population growth rate under current demographic parameters λ was estimated at 0.905 (95% CI: 0.867–0.941) under the realistic scenario and 0.928 (95% CI: 0.887–0.968) under the no dispersal scenario. Both scenarios indicate a cumulative decline of the population from 2015 to 2022 of 50.3% to 40.7%, respectively (Figure 3). Our counts of breeding pairs at the colony indicate more optimistic tendencies, a mean decline of 6.2% (5.6% at the entrance and 6.4% at the inner chambers), but with marked differences among years (Figure 3). The number of observed breeding pairs at the colony decreased by 35.9% between 2015 and 2022.

DISCUSSION

We quantify the demographic consequences of habitat selection on Mediterranean Storm Petrels, a highly philopatric and long-lived seabird species. By combining long-term individual monitoring in one of the most

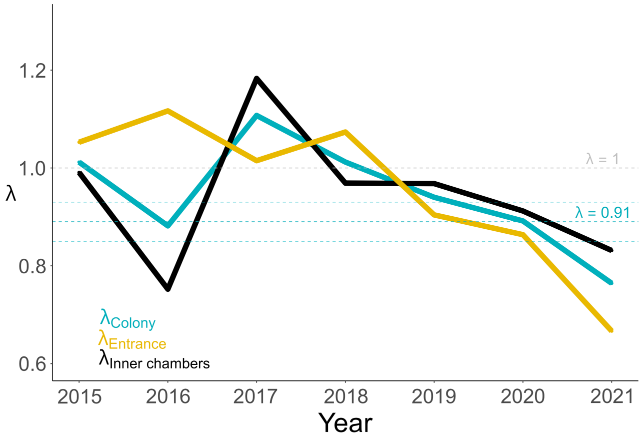

FIGURE 3 Observed and projected population growth rates for the studied Mediterranean Storm Petrel colony from Espartar Island from 2015 to 2022. The whole-colony observed λ is shown in cyan, the entrance in yellow, and the inner chambers in black. The dashed gray line depicts population stability λ = 1 and the dashed cyan line and the shaded area depict mean λ and 5th and 95th estimated percentiles, respectively.

important colonies of the Mediterranean with a robust statistical framework that accounts for state uncertainty, we assessed the effects of habitat heterogeneity on breeding success, natal fidelity, breeding fidelity, and apparent survival. Storm petrels showed dispersal mechanisms to improve their fitness but also took individual decisions that reduced it. In general, dispersal processes and in particular higher recruitment at the low-quality zone of the colony where ticks are very abundant contributed to the decline of the population.

In agreement with previous research (see Sanz-Aguilar et al., 2020), we confirmed that tick infestation was significantly higher in the low-quality breeding habitat (i.e., inner chambers) than in the high-quality breeding habitat (i.e., entrance). Mediterranean Storm Petrels breeding at the entrance showed breeding success values similar to those reported in other Mediterranean colonies with no tick infestation (Sanz-Aguilar et al., 2008, 2020; Sanz-Aguilar, Massa, et al., 2009). However, at the low-quality breeding habitat (i.e., inner chambers), more than half of breeding pairs failed reproduction annually. Breeding failure was mainly driven by nestling mortality, which was the vital rate influenced by tick infestation. Likewise, our study highlights that the apparent survival of animals breeding at the low-quality breeding habitat (i.e., inner chambers) was lower than at the high-quality habitat (i.e., entrance). This difference was slightly higher for first-time observed breeders, suggesting a potential role of experience in modulating the effects of habitat (Frankish et al., 2022). Unfortunately, given the life history of the species, the nocturnal and short time feeding behavior of the ectoparasite and the nature of the monitoring program, our data and analyses do not allow to unequivocally link the apparent survival differences to observed differences in breeding habitat quality (i.e., tick infestation). In fact, the observed differences could also respond to individual heterogeneity if lower quality individuals are relegated to lower quality habitats (Sergio et al., 2009).

Animals use social and environmental cues to maximize their fitness (Williams & Nichols, 1984). In fact, long-lived birds such as storm petrels typically prospect different breeding colonies before recruitment (Okill & Bolton, 2005). Several studies have suggested that conspecific fitness components (e.g., breeding success) can be used as a cue to guide habitat selection, with birds preferentially recruiting and/or dispersing to patches with higher fitness components (Beletsky & Orians, 1991; Boulinier et al., 2008; Forero et al., 1999). In birds, natal dispersal (i.e., between the natal and breeding sites) is typically higher both in distances and proportions of animals than breeding dispersal (i.e., between consecutive breeding events) (Greenwood & Harvey, 1982). We found that storm petrels breeding in the low-quality habitat (i.e., the inner chambers) were more likely to change nests than those breeding in high-quality habitat (i.e., the entrance), but breeding dispersal occurred at adjacent nests and dispersal of breeders between the two zones of the colony was practically nonexistent. This is consistent with previous studies, which demonstrate that bird species sometimes show anti-parasite behaviors including avoidance of nesting in sites with high parasite load (see a revision in Bush & Clayton, 2018). We also found that birds moving within zones did not experience increased breeding success. This is also consistent with the costs associated with potential mate loss or change. However, contrary to our expectation, natal fidelity was higher where fitness components were lower (i.e., the inner chambers). In fact, we did not detect any event of natal dispersal from the inner chambers to the entrance, while 38% of birds born in the entrance recruited in the inner chambers. Even if our sample size on recruits to estimate natal fidelity was small ($N = 31$ birds), no birds born at the inner chambers were detected at the entrance while the opposite occurred. The proportion of accessible nests in both areas is very similar in both areas, and our results showed higher local adult survival at the entrance. Therefore, if present, we should detect recruits from the inner chambers at the entrance in a similar proportion to, or even higher proportion than, recruits from the entrance at the inner chambers (entrance, $N = 203$; inner chambers, $N = 279$). This pattern could arise if potentially low-quality individuals from the inner chambers simply cannot get a place to breed in the competitive (high quality) habitat of the entrance. However, we think that the habitat is not saturated and competition for breeding habitat is not a limiting factor in this colony. Our data indicate that, every year during our study period, more than 30% of historical nests have been available both at the entrance and in the inner chambers. Moreover, other researchers who visited the colony 20 years ago indicated to us that breeding numbers during our study period were apparently much lower than at the beginning of the 2000s, indicating that potential nesting sites were not saturated. Thus, high breeding fidelity and the preference for recruiting at the zone of lower fitness suggested the existence of a potential evolutionary trap (Gauthier et al., 2010; Grémillet & Boulinier, 2009).

Evolutionary traps occur when animals select habitat that reduces their fitness (Schauber & Ostfeld, 2002). This is often due to rapid changes in the correlation between cues and habitat quality (Igual et al., 2007). Here, the existence of an evolutionary trap could be due to the species' high philopatry and the potential selection of deep nesting sites. In fact, petrels might not be fast enough to adaptively respond to changes in the quality of their breeding sites (i.e., varying tick infestation densities). Similar evolutionary traps have been documented for other procellariiform species, such as Cory's shearwaters (*Calonectris borealis*) (Igual et al., 2007). In that case, birds experiencing high rat predation pressure continued to experience reduced breeding success despite engaging with dispersal because individuals dispersed to adjacent areas but not to areas with lower predator density (Igual et al., 2007).

Drivers of dispersal can be multiple (Clobert et al., 2001). An extensive body of literature has described factors, aside from social information on population fitness components, that contribute to dispersal decisions (e.g., density dependence, habitat stability, food availability, mate availability, inbreeding, kin competition, dispersal costs, or individual characteristics) (Bowler & Benton, 2005; Rousset & Gandon, 2002; Travis et al., 1999; Trochet et al., 2016). It is possible that evolutionary shortcuts for dispersal decisions based on other sources of information might explain why FTBs are attracted to the inner chambers where survival and breeding success were lower. For instance, habitat stability offered by inner chambers in terms of weather, adverse oceanographic conditions (Cadiou et al., 2010) or predation by other bird species (e.g., gulls or barn owls; Guerra et al., 2014; Sanz-Aguilar, Martínez-Abraín, et al., 2009), could favor the recruitment in this zone (McPeek & Holt, 1992). Moreover, burrowing seabirds generally prefer soft or deep soil and steep slopes (Brandt et al., 1995; Carter, 1997) that are generally more available in the inner chambers (A. Sanz-Aguilar personal observation). Further, the potentially higher availability of potential mates (=widows) in the inner chambers due to a lower adult survival could promote preferential recruitment in this zone (Gauthier et al., 2010). In fact, storm petrels in Espartar started breeding at very young ages, with some birds breeding at age 1, which is rare in other colonies (Sanz-Aguilar, Massa, et al., 2009).

Although our results suggest that storm petrels at Espartar do not respond adaptively to heterogeneity in habitat quality mediated by parasite infestation in terms of dispersal, we cannot discard the hypothesis that breeding adults permanently dispersed out of the study colony. Apparent survival of experienced storm petrels breeding in the entrance is within the normal range of survival estimated for this species, but at the inner chambers of Espartar, it was lower than in other colonies of the species (Sanz-Aguilar et al., 2019; Sanz-Aguilar, Massa, et al., 2009). Moreover, our estimates of survival are apparent, and we cannot distinguish mortality from permanent emigration (Lebreton et al., 1992). For instance, massive nest desertion has been described in other seabird species experiencing high levels of tick infestation at colony sites (Duffy, 1983). Additionally, several studies suggest that infestation by ticks influences chick survival (Sanz-Aguilar et al., 2020), rather than adult survival (Khan et al., 2019; Mangin et al., 2003; Monticelli et al., 2008; Ramos et al., 2001). Accordingly, non-breeder and FTB survival did not differ between the individuals born/recruited at the two zones of Espartar colony. The similar values of non-breeder survival suggest that fledglings from the inner chambers that successfully abandoned the colony were not in poorer body condition or presented higher levels of lethal pathogens associated with ticks. However, our sample size on recruits is too small to conclude that survival of non-breeders of both areas is the same and this result must be taken with caution. In any case, the estimated survival rate of non-breeding juveniles at Espartar was much higher than that for the Benidorm colony (Hernández et al., 2017; Sanz-Aguilar, Massa, et al., 2009), suggesting that the percentage of accessible monitored nests in Espartar is much higher than in Benidorm and non-breeding survival is not very low (Sanz-Aguilar et al., 2016). The survival of FTBs was much lower than the survival of experienced birds (Breton et al., 2006; Payo-Payo et al., 2023; Sanz-Aguilar, Massa, et al., 2009; Tavecchia et al., 2001), and did not differ between zones, suggesting that habitat differences mediated by tick infestation did not cause differential immediate lethal effects on adults breeding in different areas of the colony. Differences in survival between experienced and inexperienced birds could be related to reproductive costs, as previously described in other storm petrel colonies (Sanz-Aguilar et al., 2008). Here, we think that, additionally, a high permanent emigration probability after first reproduction could explain the quite low local survival of FTBs. Finally, the hypothesis of permanent breeding dispersal causing differences in apparent survival between EBs could be reinforced by the fact that the observed dynamics are more optimistic than the estimated population growth rates, indicating that migration may also be playing an important role in the colony dynamics, as found recently for other Mediterranean procellariiformes (Sanz-Aguilar et al., 2016).

However, to verify if ticks and associated microorganisms are pathogenic for storm petrels, and thus jeopardize adult survival and population viability, additional studies are required. There is a substantial lack of knowledge on disease dynamics on wild animals, and particularly in petrels (Rodríguez et al., 2019). At the studied colony, three potential pathogens have been identified: *Borrelia turicatae* and West Nile virus in ticks (Sanz-Aguilar et al., 2020) and *Babesia* sp. (Bonsergent et al., 2022) in storm petrel blood samples (own unpublished data). There is no evidence of clinical effects on birds of *B. turicatae* or *Babesia* sp. YLG (Bonsergent et al., 2022), but other species of these parasite genera can have lethal effects on some bird species (Ebani & Mancianti, 2021). On the other hand, flaviviruses like West Nile virus are known to cause mortality of both nestling and adult birds of many bird species (Kilpatrick & Wheeler, 2019) while apparently did not cause disease in others (see Jaeger et al., 2016). The main vectors of West Nile virus are mosquitoes, but some studies suggest that soft ticks can also transmit this virus (Lawrie et al., 2004). In addition, other potential pathogens that may affect seabird health and population dynamics should also be considered (Cardoso et al., 2018). Even though we cannot unequivocally link tick's infestation to adult mortality or colony abandonment, there is no doubt that they are impacting the overall population dynamics. The estimated population growth rate is alarmingly low. Observed trends are not so pessimistic, although a clear decline is occurring, especially during the last years. The recruitment of birds born at the entrance of the colony into the inner chambers, which could compensate for the loss of breeders in this area, worsened the general expected population growth rate of the colony, making this area an important sink (Pulliam, 1988). Unfortunately, the entire colony is apparently acting as a sink. The discrepancies between observed trends and estimated population growth rates based on local demographic parameters may be indicating that immigration is also occurring, because in several years, the observed population growth rate has been much higher than the estimated one. Although petrels are widely recognized as extremely faithful species to their natal and breeding sites, current research including this study suggests that the effects of dispersal on population dynamics and persistence cannot be neglected (Sanz-Aguilar et al., 2016). Future analyses using, for example, integrated population models could clarify the extent of immigration occurring in this colony.

Here, we show how small-scale habitat selection decisions can significantly influence the long-term population dynamics of a long-lived vertebrate species. However, our results highlight that we have only begun to understand the complex interplay between intra colony heterogeneity, habitat selection, and their effects on animal demography and population dynamics. We do not have enough data to test most of these questions, but research systems where dispersal rates are higher might be able, for instance, to quantify whether the dispersal is beneficial (i.e., higher breeding success) at an individual level. Future research should focus on exploring additional environmental factors that may affect habitat selection and fitness outcomes, such as food availability, climate variability, and interspecies interactions (Cable et al., 2017). Longitudinal studies tracking individual movements and fitness across different spatial and temporal scales will be crucial to fully understand the adaptive significance of habitat selection strategies. Moreover, our findings emphasize the need to identify and quantify the long-term effects of parasites on fitness components and population dynamics, to improve our understanding of their eco-evolutionary roles in nature. Integrating this knowledge of habitat selection and its drivers into effective conservation strategies is essential. By anticipating the challenges faced by species like the Mediterranean Storm Petrel, we can develop targeted conservation actions that improve species resilience. Ultimately, our research highlights the importance of a comprehensive approach that links eco-evolutionary insights with practical conservation efforts of species in an increasingly dynamic environment.

AUTHOR CONTRIBUTIONS

Ana Payo-Payo, Andreu Rotger, Virginia Picorelli, Mariana Viñas Torres, Esteban Cardona, Oliver Martínez, and Ana Sanz-Aguilar collected the data. Ana Sanz-Aguilar conceived the idea. Ana Payo-Payo, Andreu Rotger, and Ana Sanz-Aguilar conducted the analyses. Ana Payo-Payo, Andreu Rotger, and Ana Sanz-Aguilar led the writing and all authors revised and contributed to the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Payo-Payo et al., 2025) are available from the Digital CSIC repository: https://doi.org/10.20350/digitalCSIC/17719. Code and analytical scripts used to run the analysis (Payo-Payo, 2026) are available from Zenodo: https://doi.org/10.5281/zenodo.18466662.

ORCID

Andreu Rotger https://orcid.org/0000-0002-9093-9497

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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