Effects of environmental variability and perturbations on seabirds' population dynamics.

Ana Payo Payo

Thesis 2017

Photo credit: Alan Whitehead
Ichthyaetus audouinii resting in a rock.
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Effects of environmental variability and perturbations on seabirds' population dynamics

Efectos de la variabilidad ambiental y las perturbaciones en la dinámica de poblaciones de las aves marinas

Document presented by Ana Payo Payo to fullfil the requirements of the University of Barcelona to earn a Ph.D. degree

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Menthors came in all shapes and sizes
To Ana Sanz

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Outline and publications

PhD thesis statement

This thesis is a compendium of publications, organized in four parts: Prologue, Main chapters, Epilogue, and Appendicces. The prologue presents an overview of the effects of environmental variability and perturbation on population dynamics, introduces relevant background information of the specific topics studied in this thesis, and highlights the general objectives. The second part consists of four independent chapters, each one corresponding to a different research article. Three of them are already published and a fourth one is under review. The epilogue contains a general discussion of the main findings of the thesis and the final conclusions. Finally, supplementary material and a comprehensive list of references are included.

List of accepted publications included in this thesis:

Payo-Payo, A., Oro, D., Igual, J.-M., Jover, L., Sanpera, C., and Tavecchia, G. (2015). Population control of an overabundant species achieved through consecutive anthropogenic perturbations. *Ecological Applications*, 25(8):2228–2239.
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Payo-Payo, A., Genovart, M., Bertolero, A., Pradel, R., and Oro, D. (2016). Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. *Proceedings of the Royal Society B: Biological Sciences*, 283(1829).
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J., Camps, David Ruiz-Olmo, J., and Oro, D. (Submitted). Non-lethal effects of density-independent perturbations may drive changes in age structure and reproductive value in populations: a seabird case study. *Submited to Proceedings of the Royal Society B: Biological Sciences.*

Publications summary

Chapter1

Population control of an overabundant species achieved through consecutive anthropogenic perturbations

The control of overabundant vertebrates is often problematic. Much work has focused on population-level responses and overabundance due to anthropogenic subsidies. However, far less work has been directed at investigating responses following the removal of subsidies. We investigate the consequences of two consecutive perturbations—closure of a landfill and an inadvertent poisoning event— on the trophic ecology ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), survival, and population size of an overabundant generalist seabird species, the yellow-legged gull. We expected that the landfill closure would cause a strong dietary shift and the inadvertent poisoning a decrease in gull population size. As a long-lived species, we also anticipated adult survival to be buffered against the decrease in food availability but not against the inadvertent poisoning event. Stable isotope analysis confirmed the dietary shift towards marine resources after the disappearance of the landfill. Although the survival model was inconclusive, it did suggest that the perturbations had a negative effect on survival, which was followed by a recovery back to average values. Food limitation likely triggered dispersal to other populations, while poisoning may have increased mortality; these two processes were likely responsible for the large fall in population size that occurred after the two consecutive perturbations. Life-history theory suggests that perturbations may encourage species to halt existing breeding investment in order to ensure future survival. However, under strong perturbation pulses the resilience threshold might be surpassed and changes in population density can arise. Consecutive perturbations may effectively manage overabundant species.

Keywords: Food availability, predictable anthropogenic food subsidies, seabird, population size, adult survival, pest, stable isotope analysis, anthropogenic perturbation.

Chapter2

Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird

Conditions during early life, including maternal cohort effects, can influence the future fitness of individuals. This may be particularly true for long-distance migrating birds, because, apart from conditions experienced by cohorts during rearing, conditions during early life in regions far from breeding grounds may also influence their population dynamics. Very little is known about the fitness consequences of those conditions experienced by juveniles after independence, especially in wild populations and for long-lived birds. We used multi-event capture–recapture–recovery models and a unique 26-year dataset for the Audouin's gull (*Ichthyaetus audouinii*) to assess for the first time whether survival was influenced by early conditions, both during the rearing period (i.e. a maternal cohort effect potentially affected by density dependence) and the first winter (i.e. a cohort effect driven by climate when birds disperse to wintering grounds). Our results show that juvenile survival was highly sensitive to early-life conditions and that survival decreased with stronger density dependence and harsh climate. The two consecutive cohort effects

were of similar magnitude and they may represent a selection filter. Thus, early-life conditions had a strong impact on survival, and neglecting this complexity may hinder our understanding on how populations of long-lived animals fluctuate and respond to perturbations.

Chapter3

Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers.

Studying colonisation is crucial to understand metapopulations, evolutionary ecology and species resilience to global change. Unfortunately, few empirical data are available because field monitoring that includes empty patches at large spatiotemporal scales is required. We examine the colonisation dynamics of a long-lived seabird over 34 years in the western Mediterranean by comparing population and individual data from both source and the newly-formed colonies. Since social information is not available, we hypothesize that colonisation should follow particular dispersal dynamics and personal information must be crucial in decision making. We test if adverse breeding conditions trigger colonisation events, if personal information plays a role in colonisation and if colonisers experience greater fitness. Our results show a temporal mismatch between colonisation events and both density-dependence and perturbations at the source, probably because colonisers needed a longer prospecting period to compensate for the lack of public information. Colonisers were mostly experienced individuals experiencing higher breeding success in the new colony. Our results highlight the demographic value that experienced individuals can have on metapopulation dynamics of social long-lived organisms.

Chapter4

Non-lethal effects of density-independent perturbations may drive changes in age structure and reproductive value in populations: a seabird case study.

Intensification of perturbation regimes due to global change should increase environmental variability experienced by individuals that may cause larger changes in population dynamics. For instance, perturbations can affect population dynamics through lethal effects by significantly increasing mortality. However, the role of non-lethal effects causing disturbance such as physiological stress (potentially affecting breeding performance) and behavioural responses has been comparatively overlooked and their potential population effects remain obscure. During the last 23 years we developed a mark-recapture program for the Audouin's gull (*Ichthyaetus audouinii*) and an intensive carnivore monitoring — a rare combination of long-term datasets — to assess how non-random dispersal as a non-lethal effect of the appearance of predators in a previously predator-free area may affect population dynamics. Specifically, we evaluate changes in age structure, breeding performance and colonization-extinction turnover of discrete breeding patches within the colony. Once predators entered the colony, the number of occupied patches increased together with the rate of patch extinction; individuals responded behaviourally by moving to less accessible areas to predators. More importantly from a demographic point of view, presence of predators caused differential breeding dispersal by experienced, better performing breeders being more prone to leave the colony. This differential dispersal modified the age structure and reduced the reproductive value of the population. The role of non-lethal effects for population dynamics might be more important than previously thought, especially under scenarios of global change that predict increases in magnitude and frequency of perturbations, such as invasive predators.

Supervisors' report

Dr. Daniel Oro de Rivas, Professor of Research at CSIC at IMEDEA (CSIC-UIB), Esporles, Mallorca (Spain), as PhD supervisor of the Ph.D. Thesis authored by Miss Ana Payo-Payo entitled: Effects of environmental variability and perturbations on seabirds' population dynamics.

INFORMS:

That the results and conclusions achieved in the research developed by Miss Ana Payo-Payo as part of her Ph.D. Thesis have been organized in 4 chapters which correspond to 3 publications and 1 manuscripts (in review round). Following, the list of publications and manuscripts is shown indicating the journal impact factor IF (according to SCI of ISI Web of Knowledge, Journal citation Report-2015.

List of accepted publications included in this thesis: Payo-Payo, A., Oro, D., Igual, J.M., Jover, L., Sanpera, C., and Tavecchia, G. (2015). Population control of an over-abundant species achieved through consecutive anthropogenic perturbations. Ecological Applications. DOI: 10.1890/14-2090.1 Impact factor: 4.55.

Payo-Payo, A., Genovart, M., Bertolero, A., Pradel, R., and Oro, D. (2016). Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. Proceedings of the Royal Society B: Biological Sciences, 283(1829). DOI: 10.1098/rspb.2015.3042 Impact factor: 6.42.

Payo-Payo, A., Genovart, M., Sanz-Aguilar, A., Greno, J., Garcia-Tarason, M., Bertolero, A., Piccardo, J., and Oro, D. Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers. In press: Scientific Reports Impact factor: 5.228.

List of submitted publications included in this thesis:

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CERTIFIES:

That Miss Ana Payo-Payo contribution has been very active, as it is demonstrated by her participation in the definition of the objectives and the focus of the research and its derived manuscripts. Miss Ana Payo-Payo is first author in the 4 final manuscripts. Finally, I certify that any of the co-authors of the manuscripts detailed above has used, neither is going to be use, implicitly or explicitly, the information produced and presented here with the purpose of elaborating another Ph.D. Thesis.

Barcelona, 26 de Gener 2017

Daniel Oro

I | Prologue

General introduction

Population ecology, an overview

Population concept has been absolutely indispensable for the progress of ecology (Hanski 1999). Understanding the relationships between the dynamic of animal populations and the variability of their environment has fascinated ecologists for decades and is a central concern of both theoretical and applied ecology (Sibly et al. 2003). Population ecology, focuses on the study of how life history traits of those individuals constituting populations relate to their environment and respond to changes (Park 1946, Rockwood 2006). The basic unit conforming populations is the individual (Tujlapurkar and Caswell 1997). Individual organisms are born, grow develop, mature, move, reproduce and eventually die (Tujlapurkar and Caswell 1997). Demographic heterogeneity among individuals (e.g. age, sex or experience) can lead to variation in their relationships between vital rates, density or environmental variability, therefore is crucial for population dynamics (Tujlapurkar and Caswell 1997, Coulson et al. 2001b). A wide range of these relationships have been studied by population ecologists, including description of processes such as population growth, population equilibrium, prey-predator dynamics, density-dependent population regulation, Allee effects, dispersion, epidemiology or population viability analyses (Park 1946, Hanski and Gilpin 1997, Rockwood 2006). An important subset of these analyses concludes that the demographic components of a life history vary temporally and that population dynamics are a result of complex interactions between population structure, population density and environmental variability (Tujlapurkar and Caswell 1997, Coulson et al. 2001a). Although much progress has been made in population ecology are still numerous questions that need to be addressed. For instance, an interesting and promising question that remains unsolved is to disentangle what are the mechanisms that determine abundance and population persistence in increasingly variable environments — particularly in the face of extreme events or perturbations.

Environmental variability and perturbations

Perturbation studies are common in the literature and its effects across organization levels have been widely described. It is surprising how intuitive seems to distinguish what a perturbation is in the context of a particular system, yet it remains a challenge to formally define when environmental variability becomes a perturbation. Many authors attempted to provide a general definition and, despite there is lack of consensus, a few common characteristics aroused from all definitions (Table 1). First, most definitions neglect that for some systems long-term persistence depends on periodic disturbance, as for example, fire-dependent vegetation and the perspective of perturbations as an source of adaptation potential is rarely considered (Pickett et al. 1989, Shea et al. 2004, Gallopin 2006).

Table 1: Examples of perturbation definitions across the literature.

Definition	Reference
· Partial or total destruction of biomass.	(Grime 1977)
· Disruption of the pattern of the ecosystem, principally by external physical forces.	(Bormann and Likens 1979)
· Any deviation, or displacement, from the "nominal state" in structure or function at any level of organization.	(Odum et al. 1979)
· Patch birth rate, and mean and maximum size at birth can be used as adequate indices of disturbance.	(Paine and Levin 1981)
· A selective alteration of the density of one or more members of the community.	(Bender et al. 1984)
· A discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.	(Sousa 1984)
· Any relative discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment.	(Pickett and White 1987)
· A change in the minimal structure caused by a factor external to the level of interest.	(Pickett et al. 1989)
· Process that alters the birth and death rates of individuals present in the patch.	(Petraitis et al. 1989)
· Primarily non-biotic, stochastic events that results in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organisation and ecological equilibrium; such events are understood to operate through the medium of weather and at the frequency scale of algal generation times.	(Reynolds et al. 1993)
· A force often abrupt and unpredictable, with a duration shorter than the time between disturbance events, that kills or badly damages organisms and alters the availability of resources.	(Mackey and Currie 2000)
· An event which alters the niche opportunities available to the species in a system. This will often be an event which destroys or removes biomass, freeing up resources for other organisms to use.	(Shea et al. 2004)
· A discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established. Disturbance should be ecologically relevant for the system under study.	(Svensson 2010)
· Relative discrete events that harm the affected organisms.	(Fox 2013)

This negative perception of perturbations is probably related to the fact that perturbations often involve an element of damage or destruction (Rykiel 1985). In general definitions fail to account for the fact that environmental conditions fluctuate on both temporally and spatially, and that populations — species, ecosystems, or the organization level considered — are assumed to have evolved the ability to withstand and respond differentially to such variability, therefore to endure to perturbations (at least to some extent). Second, either explicitly stated or not, perturbations are usually defined with regard to a reference state — either a previous or an 'optimum' state — and a spatio-temporal scale (Rykiel 1985, Poff 1992). The definition of these reference state and spatio-temporal scale are crucial — it also seems to me the reason behind the lack of general definition — since the provides the necessary context to evaluate if a perturbation will be ecologically or/and evolutionary meaningful. Anyway, I found more interesting than the formal definition itself that these common characteristics of most definitions evidence a strongly anthropocentric — therefore, biased — perception of ecological processes such as perturbations.

Above, I explored common characteristics of historical definitions of perturbations across the literature. The aim of this thesis however is not to define perturbations — it appears to me more as a philosophical that an ecological debate — but to better understand the consequences of these new perturbation regimes on populations dynamics and discuss its implications for populations persistence. Here, I will approach perturbations as the result of two sequential events: first, disrupting forces are applied to a population, disturbances; which are followed by series of reactions to such disturbances, responses (Lake 2003). Disturbances are seldom static and vary spatio-temporally, so will do population responses (Coulson et al. 2001a). This variability makes the study of perturbations an inherently multidimensional and nonlinear problem (Paine et al. 1998, Miller et al. 2011).

Effects of perturbations on population dynamics

Natural populations are the product of a long history of coevolution of their constituents with the environment (May 2001). However, humans have deeply transformed the planet causing regional and global effects and it is now clear that such changes are an important driving force on natural populations (Vitousek et al. 1997, Walther et al. 2002, Parmesan and Yohe 2003, Halpern et al. 2008). In this context, under current scenarios of global change, questions such as how populations will cope to future perturbation regimes have become especially popular. Particularly relevant in the context of ecological — and population — responses is the increased spatio-temporal heterogeneity through asymmetry in regional changes and increased frequency and intensity of extreme events (Walther et al. 2002, Schellnhuber 2006). Increased heterogeneity will likely impact population dynamics and have strong implications for non-linear processes (Walther et al. 2002, Schellnhuber 2006). It is plausible that co-evolutionary processes, between individuals and the environment, sought out regions of demographic parameter space which were previously compatible with long-term persistence, yet how populations will persist under new perturbation regimes remains an open question (Vitousek et al. 1997, May 2001, Halpern et al. 2008). Populations will face both predicted and potentially surprising events — not yet currently envisioned — because of the enormous complexities of the processes and interrelationships involved and our insufficient understanding of how such processes work both individually and collectively (Schneider et al. 1998, Schellnhuber 2006).

Forecasting population responses and population persistence under new perturbation regimes can be of special importance when species are considered pests or endangered species (Oro et al. 2013a). Moreover, environmental policies aiming to mitigate the human effects pose both threats and opportunities for human dominated ecosystems (Bicknell et al. 2013). For instance, upcoming reform of the European Union Common Fisheries Policy (CFP) will drastically reduce food availability for scavengers (Bicknell et al. 2013). Such measures aim to promote healthier ecosystems, but they also constitute large scale experiments to study the effects of perturbations on ecological processes such as resilience, extinction thresholds, competition and extinction cascades. Much work has been developed to assess population stability and resilience properties in the face of single perturbations. However, we do not have a clear understanding of the roles of short-term versus long term environmental stochasticity or consecutive perturbations in population dynamics.

Seabirds as a study model

Population ecologists tend to see species as a tool, a model with representative properties of an organization level — rather than as a single species itself — that allows them studying higher ecological processes. Almost any taxonomic group could be potentially selected as a study model depending on the ecological question to resolve. However, there are a few characteristics that make some species such as seabirds a particularly good study model to assess the effects of environmental variability on population dynamics. New perturbation regimes are known to have caused worldwide changes in ecosystems. These changes should be evident, especially in species at higher levels in food chains, which might integrate and/or amplify their effects (Croxall et al. 2002). Seabirds are highly mobile top predators (Schreiber and Burger 2001). Moreover, seabirds are usually social long-lived species characterized by low reproductive rates and high adult survival rates (Schreiber and Burger 2001). Life-history theory predicts that the key parameter driving their population functioning is adult survival; however, juvenile survival has recently been acknowledged as an important source of variability (Gaillard et al. 1998, Grande et al. 2009, Sergio et al. 2011). Therefore, seabirds life-strategy has evolved towards long generation times which makes them especially vulnerable to environmental change (Louzao 2006). Moreover, they spend most of their lives at sea but they regularly come ashore (to coastal areas) to breed, which results in exposure to a wide range of marine and terrestrial perturbations (Schreiber and Burger 2001, Paleczny et al. 2015). Moreover, since they are relatively easy to monitor and they are often considered flagship species, they are exceptionally well-studied comparted to other vertebrate groups (Schreiber and Burger 2001, Bennett and Owens 2002, Croxall et al. 2012, Paleczny et al. 2015). In summary, they are an excellent model to assess the effects of environmental variability and perturbations on population dynamics because they are particularly well-studied, their life-history traits makes them more vulnerable to multiple perturbations and their ecology integrates large spatio-temporal scales processes (Paleczny et al. 2015).

This thesis focuses on the study of perturbations on a particular family of seabirds, the gulls. Among seabirds, gulls are one of the least specialized groups and show some particularities with regard to foraging, breeding and movement ecology. Gulls are generalists, opportunistic and omnivorous species that feed in a wide range resources such as insects, squid, crustaceans, molluscs, earthworms, small mammals, seeds, fruits, human refuse or fishing offal (Del Hoyo et al. 1996). Even though most seabirds have low reproductive rates most gulls have a comparatively large clutch size of three eggs (Del Hoyo et al. 1996). Gulls tend to move towards warmer regions during winter. However, they usually cover shorter distances than other seabird species such as Procelariforms (Del Hoyo et al. 1996). Therefore, they are often considered nomadic rather than migratory species (Del Hoyo et al. 1996). Finally, gulls share many habitats with human populations, as a consequence of this tight contact, gulls have been often considered as pest (Del Hoyo et al. 1996). Social interest in controlling gull populations has resulted in the implementation of numerous programs aiming to control their numbers and in the production of vast literature about their biology which makes them a perfect model for studying the effects of consecutive perturbations on population dynamics (Sanz-Aguilar et al. 2009a,b).

Sources of disturbance:

As we mentioned above seabird populations face a wide range of marine and terrestrial threats. The main current threats at sea are posed by commercial fisheries and pollution, whereas on land, alien invasive predators, habitat degradation and human disturbance are the main threats (Croxall et al. 2012). As a result, seabirds are more threatened than other comparable groups of birds, their status has deteriorated faster over recent decades (Croxall et al. 2012). Here, I explain how different disturbances (specifically studied in this thesis) can affect seabirds population dynamics. In particular, climate change, predictable anthropogenic food subsidies or inter- and intra- specific interactions. The disturbances described below will potentially cause three non-exclusive effects, seabird populations will either modify their breeding and foraging ecology to survive and reproduce within the same distribution zone, modify their distribution, or die (Gremillet and Boulinier 2009). Current research has revolutionised our perception of seabird ecology and there are quite a few evidences of the ability of seabirds to buffering changes in environmental stochasticity (Crawford 2009, Crawford et al. 2015). However, behavioural and phenotypic plasticity might have physiological limits and beyond a certain threshold species and populations might not be able to cope with changes (Crawford et al. 2015).

Climate change

Cyclic and extreme events are inherent to natural ecosystems and seabirds have evolved in this fluctuating environment. However, there are clear evidences that human activities have triggered global warming and resulted in increases in environmental stochasticity (Alley et al. 2003, Halpern et al. 2008). Despite the uncertainty about the overall effects of such changes, ecological responses to recent climate change are already visible (Walther et al. 2002). Climate change has lead responses in the composition, structure and dynamics of ecosystems, the distributions of species/populations and the phenology and physiology of organisms (Walther et al. 2002). For instance, there has been significant decreases in primary productivity, with important cascading effects on food availability of marine top-predators (Hutchings et al. 2009, Lindegren et al. 2013). Large-scale climatic phenomena such as El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation(NAO) and anomalies in oceanographic such as Sea Surface Temperature(SST) and sea ice extent have also driven changes in species foraging areas, high mortality and breeding failure of seabirds (Barbraud and Weimerskirch 2001, Stenseth et al. 2003, Jenouvrier et al. 2005). Furthermore, there are evidences that climate change might have synergic interactions with other natural and anthropogenic perturbations increasing the complexity of ecological interactions (Walther et al. 2002, Gremillet and Boulinier 2009).

Predictable anthropogenic food subsidies — PAFS

PAFS have important ecological and evolutionary implications for populations (Oro et al. 2013a). They affect ecosystems by altering processes such as competition, predator-prey dynamics and biogeochemical cycles (Oro et al. 2013a). PAFS are highly spatio-temporally predictable compared to the stochastic fluctuations inherent to natural systems (Oro et al. 2013a). Once present they cause homogenization of environment by reducing spatio-temporal variability of populations and increase resilience of opportunistic species (Bicknell et al. 2013). Although, high predictability can be translated into higher stability; higher stability does not necessarily imply higher resilience (Holling 1973). The odds of persistence might be reduced since population fluctuations are essential to respond to perturbations (Holling 1973). At population level, availability of high spatio-temporal predictable food has strong effects on population structure and dynamics, their presence usually results in increases of breeding success, survival, population size and changes in dispersal (Oro et al. 2013a).

Moreover, they can trigger changes in the behavioural and morphological differences across populations, leading to changes in gene frequency (Yom-Tov 2003). Landfill sites and fishing discards are the two of the main PAFS in terms of food availability and global distribution (Oro et al. 2013a). Measures towards their reduction have started to be implemented worldwide. For instance, modifications of the Landfill Waste Council Directive (LWCD) and Common Fisheries Policy (CFP) that respectively aim to put an end to open-air landfilling and enforce the landing of fishing discards (Parliament 2013, E.U. 2009, European-Commission 2008). However, such management measures aiming to mitigate the consequences of the human disturbance can also become an disturbance themselves and a challenging but interesting question is to disentangle how will populations exploiting PAFS will respond to changes in their availability (Oro et al. 2013a, Sarda et al. 2015).

Inter- and intra- specific biotic interactions:

Predation

Predation is a major source of heterogeneity in the structure and dynamics of natural populations and an agent of natural selection in the evolution of life histories (Sousa 1984). The introduction of alien and native invasive species as a result of human activities has been extensively associated with extinctions and declines of seabird populations (McCreless et al. 2016). Seabirds have evolved towards breeding in predator free environments, therefore they lack of appropriate behavioural responses to predation and they often suffer from both lethal and non-lethal effects of predation (Wanless et al. 2007). Sometimes predation acts removing already — doomed individuals — from the population which might have no effect on population densities; however, it can also cause additive mortality and lead to population crashes. Non-lethal effects such as disturbance or physiological stress can also trigger changes in the distribution, abundance and interactions between individuals and leading to changes in population dynamics (May and McLean 2007). Especially interesting are the consequences of the differential effects of predators presence on individuals — depending characteristics such as age, sex or experience classes. Such heterogeneity can affect the long-term population dynamics by changing the ability of populations to adapt to current and future environmental change (Teitelbaum et al. 2016).

Density-dependence

Another central issue in ecology is the effects of density dependence on population regulation and its interaction with environmental variability (Tujlapurkar and Caswell 1997, Coulson et al. 2001b, May and McLean 2007). Density dependence can arise in natural populations as a result of interactions with other members of the system — for instance in the form of competition for resources. Density-dependent effects will be especially important after a period with favourable environmental conditions which might have allow population numbers to increase, then density-dependent effects and their interactions with upcoming extreme environmental events such as perturbations will arise (Coulson et al. 2001b). It is also important to understand that even populations that might apparently been density-independent might, in fact, be subject to delayed density dependent effects and that such lagged responses are often a destabilizing force for population dynamics (Turchin 1990, May and McLean 2007). Understanding and recognising the importance of the (non-linear) interactions between human and natural environmental disturbances and density-dependence is essential to disentangle the population functioning under different perturbation regimes.

Models and modelling: a general methodological framework

The study of populations dynamics is a challenging enterprise. First, because it requires complex mathematical modelling and computational power and second because it requires maintaining long-term monitoring of wild populations which is both economically and logistically demanding. The overarching objective of population ecology and specifically of ecological modelling is always to help make sense of what we observe in the field. Thus the theoretical framework and statistical tools we used to address each specific research question depends on our immediate goals (Tujlapurkar and Caswell 1997). In the abovementioned sections I have tried to provide a theoretical framework and ecological context of my thesis. Now, I will describe the statistic tools I have selected to test specific hypotheses about the effects of consecutive perturbations on different populations.

I would like to underline that although much of the methodology in this thesis uses linearization techniques — an obvious oversimplification of reality — the importance of the consequent non-linear responses arising from perturbations is emphasized. Moreover, I do not intend to be comprehensive in the methodological description; I have done that in each specific chapter. Instead, I'll try to give a clear and brief explanation of the different methodologies I have used.

Capture recapture recovery models

Robust estimation of population densities, survival and movement rates usually — but not necessarily — entails capturing and marking individuals so they can be recognized at subsequent encounters. Here, I used capture recapture recovery approaches to estimate population numbers and survival probabilities (Lebreton et al. 1992). Population numbers were estimated though Petersen-Lincoln methodologies and survival analyses were performed using both multistate and multievent frameworks (Pradel 2005). The former allows estimation of survival and transition probabilities from unobservable states (Kendall and Nichols 2002, Pradel et al. 2005, Conn and Cooch 2009). The later allows to incorporate uncertainty about the state in which an animal is found upon capture (Pradel 2005).

Stable isotope analyses

Stable isotope analyses were first used to disentangle past diets in the late 1970's (DeNiro and Epstein 1978). Since then major advances have occurred both in instrumentation and understanding the processes that cause variation in stable isotope abundance ratios in different substances (Forero et al. 2005, Caut et al. 2009, Ramos et al. 2009b). They are now an extremely popular tool in diet analyses that allows accurate discrimination between trophic levels, foraging areas and food sources (Hobson 1987, Forero et al. 2005, Caut et al. 2009).

From linear regressions to general linear mixed models

Linear regression models allow exploring the relationship between a dependent and an explanatory variable. Together with their multivariate generalization they have been extensively use in ecological studies and allowed to address numerous ecological questions. However, data sets in ecology often don't match the assumptions of normally distributed data required by classical statistical frameworks (Bolker et al. 2009). Deviation from such assumptions should not prevent us from analysing atypical data, which can be managed with generalized linear mixed models (GLMMs). GLMMs combine the properties of two statistical frameworks — linear mixed models and generalized linear models — and as a result are an extremely powerful tool for analysing non-normal data that involve random effects (Bolker et al. 2009).

Breaking point analyses

Finally, when analysing the effects of environmental variability, we often we face challenges beyond quantification of the relationship of one or multiple variables. Often we also need to identify specific thresholds that determine ecosystem or regime shifts and breaking point analyses has arisen in the last couple of decades as a powerful tool for addressing such questions.

Overarching thesis aim and thesis outline

The overarching aim of this thesis is to explore the effects of environmental variability and perturbations on the demography of marine top predators (i.e. gulls) across different spatio-temporal scales. Specifically, I explore the effects of climate, PAFS and biotic interactions such as density-dependence and predation. This thesis is structured in 4 main chapters (Chapters 1-4) that are coherent and addresses a different biological question and a final chapter (Chapter III) that summarizes the conclusions of this thesis, discusses possible improvements and provides and outlook for future work. A list of literature references is provided at the end of the document.

Below I outline the particular objectives addressed in Chapters 1 to 4:

- In Chapter 1 I evaluated the consequences of consecutive perturbations — namely, the termination of predictable food subsidies and a stochastic mortality event — on the trophic ecology, survival, and population size of a so-called overabundant generalist seabird species, the yellow-legged gull (*Larus michahellis*). To achieve these objectives, I first estimated diet composition and temporal variation in the feeding ecology of yellow legged gulls by means of stable isotope analysis. Then, using multistate modelling framework and capture-mark-recapture-recovery data, I estimated local adult survival and I addressed potential short and long term effects of consecutive perturbations. Finally, I evaluated potential changes on population trends.

- In Chapter 2 I explored potential survival costs of consecutive cohort effects during early life in a long-lived bird, the Audouin's gull (*Ichthyaetus audouinii*). More specifically I tested effects of a maternal cohort effect potentially affected by density-dependence and a cohort effect driven by climate at wintering grounds during the first winter. In this case, I analysed a 26-year capture-recapture-recovery dataset on Audouin's gulls breeding at Ebro Delta using a multievent modelling approach to account for unobservable processes and recapture heterogeneity. To my knowledge, this is the first attempt to model long and short term survival costs driven by conditions during two critical early life periods, the rearing phase and the first winter.

- In chapter 3 I examined colonization dynamics of a long-lived seabird, the Audouin's gull during the last three decades along the western Mediterranean coast. By doing so, I first aim to provide some insights on the relationship between perturbations and adverse breeding conditions and colonization events. Therefore, I used breaking point analysis to identify changes in the colonization process and qualitatively associate it to perturbations or adverse breeding condition events. Second, I assessed the role of private information (i.e. breeding experience) on the colonization processes. Finally, I evaluated fitness consequences (i.e. in terms of breeding success) of the colonization process.

- In chapter 4 I studied the role of non-lethal effects of predation on population persistence. I used a 23-year long-term mark-recapture dataset for the Audouin's gull to assess whether disturbance and dispersal may compromise long-term populations persistence. Specifically, we quantified changes in age structure, breeding performance (egg volume, clutch size and breeding success) and re-location of breeding areas within the Ebro Delta breeding site.

Introducción general (Castellano)

Ecología de poblaciones, una visión de conjunto

El concepto de población ha sido absolutamente indispensable para el progreso de la ecología (Hanski 1999). Durante décadas los ecólogos han estado fascinados intentando entender las relaciones entre la dinámica de poblaciones y la variabilidad ambiental , siendo por ello una preocupación clave para la ecología teórica y aplicada (Sibly et al. 2003). La ecología de poblaciones se centra en el estudio de los rasgos de vida de los individuos que constituyen las poblaciones y cómo estos se relacionan con su ambiente y los cambios que en el se producen (Park 1946, Rockwood 2006). El individuo es la unidad básica que conforma las poblaciones (Tujlapurkar and Caswell 1997). Los individuos nacen, crecen, maduran, se mueven, se reproducen y finalmente mueren (Tujlapurkar and Caswell 1997). La hetereogeneidad demográfica entre individuos (p.e. edad, sexo o experiencia) es clave en la ecología de poblaciones porque puede dar lugar a variaciones en las relaciones entre rasgos de vida entre, o de esos mismos rasgos con la densidad de individuos o la variabilidad ambiental (Tujlapurkar and Caswell 1997, Coulson et al. 2001b). Los ecólogos de poblaciones han estudiado una gran variedad de estas relaciones, incluyendo la descripción de procesos como el crecimiento poblacional, equilibrio poblacional, dinámicas depredador–presa, procesos denso–dependientes de regulación de poblaciones, efectos Allee, dispersión, epidemiología o análisis de viabilidad de poblaciones (Park 1946, Hanski and Gilpin 1997, Rockwood 2006). Una gran parte de estos estudios concluye que los rasgos vitales presentan variabilidad temporal y que la dinámica de poblaciones es resultado de las interacciones complejas entre la estructura de las poblaciones, la densidad de las mismas y la variablidad ambiental (Tujlapurkar and Caswell 1997, Coulson et al. 2001a).

A pesar de los grandes progresos realizados en ecología de poblaciones, aún quedan muchas preguntas sin responder. Por ejemplo, una de las cuestiones más prometedoras e interesantes que aún no ha sido resuelta son los mecanismos que determinan la abundancia y persistencia de las poblaciones en ambientes cada vez más variables — especialmente frente a eventos extremos y/o perturbaciones.

Variabilidad ambiental y perturbaciones

Los estudios relativas a las perturbaciones son comunes en la literatura científicas y sus efectos están relativamente bien descritos en los diferentes niveles de organización biológica. Es sorprendente lo intuitivo que parece distinguir lo que es una perturbación en el contexto de un sistema definido, sin embargo, definir cuando la variabilidad ambiental se convierte en una perturbación supone un gran reto. Muchos autores han intentado formular una definición general y a pesar de la falta de consenso, hay algunas características comunes a casi todas las definiciones (Table 2). En primer lugar, la mayoría de las definiciones parecen ignorar que en algunos sistemas la persistencia a largo plazo depende de la perturbación periódica del sistema, es el caso de la vegetación pirófita, y la visión de las perturbaciones como una fuente de potencial adaptativo es rara vez considerada (Pickett et al. 1989, Shea et al. 2004, Gallopin 2006).

Table 2: Ejemplos de definiciones de las perturbaciones en la literatura científica.

Definition	Reference
· Destrucción parcial o total de biomasa.	(Grime 1977)
· Ruptura del patron del ecosistema, principalmente debido a fuerzas físicas externas.	(Bormann and Likens 1979)
· Desviación, o desplazamiento, del 'estado nominal' en la estructura o función a cualquier nivel de organización.	(Odum et al. 1979)
· La tasa de nacimientos de un área, y su tamaño medio y máximo al nacer pueden ser usados como ínidices de la alteración.	(Paine and Levin 1981)
· Una alteración selectiva de la densidad de uno o más miembros de la comunidad.	(Bender et al. 1984)
· Daño, desplazamiento o muerte puntual y discreta de uno o más individuos (o colonias) que directa o indirectamente crea una oportunidad para nuevos individuos (o colonias) para establecerse.	(Sousa 1984)
· Cualquier evento discreto en el tiempo que altera un ecosistema, comunidad o estructura poblacional y cambia los recursos y sustratos disponibles, o el medio físico.	(Pickett and White 1987)
· Un cambio en la estructura mínima causado por un factor externo al nivel de interés.	(Pickett et al. 1989)
· Proceso que altera las tasas de nacimiento y mortalidad de individuos en el área considerada.	(Petraitis et al. 1989)
· Eventos no bióticos y estocásticos que resultan en la alteración y cambios abruptos en la composición y que interfieren con procesos internos relativos a la auto-organización y al equilibrio ecológico. Se entiende que dichos eventos operan a través de las condiciones ambientales y de la escala de la tiempo de generación de las algas.	(Reynolds et al. 1993)
· Una fuerza a menudo abrupta y no predecible, con una duración más corta que el tiempo entre dos alteraciones, que mata o daña organismos y altera la disponibilidad de recursos.	(Mackey and Currie 2000)
· Un evento que altera las oportunidades de una especie de encontrar un nicho en un sistema. A menudo es un evento que causa destrucción o eliminación de biomasa, liberando recursos para el uso de otros organismos.	(Shea et al. 2004)
· Daño, desplazamiento o muerte puntual de uno o más individuos (o colonias) que directa o indirectamente crea la oportunidad para nuevos individuos (o colonias) para establecerse. La alteración debe ser ecológicamente relevante para el sistema de estudio.	(Svensson 2010)
· Evento relativamente discreto que daña los organismos afectados.	(Fox 2013)

Esta percepción negativa de las perturbaciones está probablemente relacionada con el hecho de que las perturbaciones por lo general causan daño o destrucción (Rykiel 1985). Por norma general, las definiciones no tienen en cuenta el hecho de que las condiciones ambientales fluctúan tanto espacial como temporalmente, y que las poblaciones — especies, ecosistemas o el nivel de organización considerado — han evolucionado para resistir y responder de manera diferencial a dicha variabilidad. Por lo tanto han evolucionado para soportar las perturbaciones (al menos hasta cierto punto). En segundo lugar, en todas las definiciones se incluye bien sea explicita o implícitamente un estado de referencia — ya sea con respecto a un estado previo o a un estado óptimo — y una escala espacio temporal (Rykiel 1985, Poff 1992). La definición del estado de referencia y la escala espacio temporal son cruciales ya que describen el contexto necesario para evaluar si una perturbación tendrá consecuencias a escala ecológica y/o evolutiva. Además, desde mi punto de vista, la necesidad de definir estas referencias en cada caso es la causante de la falta de una definición general. En cualquier caso, la definición formal de las perturbaciones es menos interesante que las implicaciones que se derivan de las características comunes de todas las definiciones. Todas ellas presentan una visión antropogénica — y por lo tanto sesgada — de procesos ecológicos como las perturbaciones.

En el párrafo anterior, he explorado en la literatura las definiciones de perturbaciones y sus características comunes. El objetivo de esta tesis sin embargo no es definir las perturbaciones — ese es un debate más filosófico que ecológico — sino intentar entender las consecuencias de los nuevos regímenes de perturbaciones en la dinámica de poblaciones y discutir sus implicaciones para el modelado ecológico. En esta tesis enfocaré el estudio de las perturbaciones como el resultado de dos eventos consecutivos: primero, la población sufre el impacto de fuerzas naturales o antrópicas, una alteración, a la que la población reacciona con una serie de respuestas (Lake 2003). Las alteraciones rara vez son estáticas y varían espaciotemporalmente, al igual que las respuestas poblacionales (Coulson et al. 2001a). Esta variabilidad hace de el estudio de las perturbaciones un problema inherentemente multidimensional y no-lineal (Paine et al. 1998, Miller et al. 2011).

Efectos de las perturbaciones en la dinámica de poblaciones

Las poblaciones naturales son el resultado de una larga historia coevolutiva entre sus constituyentes y el medio que les rodea (May 2001). El hombre ha transformado intensamente el planeta causando intensos cambios a escala local y global y hoy en día está claro que dichos cambios tienen un impacto en las poblaciones (Vitousek et al. 1997, Walther et al. 2002, Parmesan and Yohe 2003, Halpern et al. 2008). En este contexto, y teniendo en cuenta las previsiones de cambio global, ciertas preguntas se han hecho extremadamente populares, por ejemplo si las poblaciones serán capaces de hacer frente a la intensificación de los regímenes de perturbaciones. Especialmente relevantes son las respuestas poblacionales al incremento de la heterogeneidad espacio-temporal como resultado de la asimetría en los cambios regionales y la intensificación de la magnitud y periodicidad de los eventos extremos (Walther et al. 2002, Schellnhuber 2006). El aumento en la heterogeneidad tendrá implicaciones en la dinámica de poblaciones pero sobretodo en los procesos no-lineales (Walther et al. 2002, Schellnhuber 2006). Es possible que los procesos co-evolutivos entre los individuos y su ambiente, definieran regiones del espacio de parámetros demográficos, compatibles con la persistencia a largo plazo, sin embargo si las poblaciones serán capaces de persistir bajo los nuevos regímenes de perturbaciones es incierto (Vitousek et al. 1997, May 2001, Halpern et al. 2008). Las poblaciones se enfrentaran a estos eventos ya previstos pero también a otros imprevistos debido a la gran complejidad de los procesos e interrelaciones, así como a nuestra falta de entendimiento sobre como los procesos tienen lugar a nivel individual y colectivo (Schneider et al. 1998, Schellnhuber 2006).

Paradójicamente, predecir las respuestas poblacionales y la persistencia de las mismas bajo los nuevos regímenes de perturbaciones es especialmente importante cuando hablamos de especies invasoras (pestes) y las especies protegidas (Oro et al. 2013a). Además, las políticas ambientales implementadas para reducir los efectos antrópicos en el medio natural suponen al mismo tiempo amenazas y oportunidades en los ecosistemas antropizados (Bicknell et al. 2013). Por ejemplo, la reciente reforma de la Política Pesquera Europea reducirá dramáticamente la disponibilidad de alimento para las especies carroñeras (Bicknell et al. 2013). Dichas medidas pretenden conseguir ecosistemas más saludables, sin embargo también constituyen experimentos a gran escala para estudiar los efectos de las perturbaciones en procesos ecológicos como la competencia, la resiliencia, los umbrales de extinción y las extinciones en cascada. Mucho trabajo se ha llevado a cabo para estudiar propiedades como la resiliencia y la estabilidad de las poblaciones frente a perturbaciones individuales. Sin embargo, aún no existe un conocimiento claro de el papel de la estocasticidad ambiental a corto y largo plazo o de los efectos de perturbaciones consecutivas en la dinámica de poblaciones.

Las aves marinas como modelo de estudio

Los ecólogos de poblaciones tendemos a ver a las especies como herramientas, modelos representativos de las propiedades y características de un determinado nivel de organización — más que como una especie como tal — lo que nos permite estudiar procesos ecológicos. Prácticamente cualquier grupo taxonómico podría ser seleccionado como modelo de estudio en función de la pregunta a responder. Sin embargo, hay una serie de características que hacen a algunas especies, como por ejemplo las aves marinas, modelos especialmente buenos para estudiar los efectos de la variabilidad ambiental en la dinámica de poblaciones. Como decía anteriormente la intensificación de la magnitud y frecuencia de los eventos extremos ha provocado importantes cambios en los ecosistemas. Estos cambios son especialmente evidentes en especies que se encuentran en niveles altos de la cadena trófica ya que integran y amplifican dichos efectos (Croxall et al. 2002). Las aves marinas son depredadores apicales con gran movilidad (Schreiber and Burger 2001). Además, las aves marinas suelen ser coloniales, longevas y se caracterizan por tener un éxito reproductor bajo y alta supervivencia adulta (Schreiber and Burger 2001). La teoría de historia de vida predice que la supervivencia adulta es el parámetro demográfico clave para el funcionamiento de las poblaciones; sin embargo, estudios recientes han señalado que la supervivencia juvenil también es una fuente importante de variabilidad (Gaillard et al. 1998, Grande et al. 2009, Sergio et al. 2011). Las aves marinas han evolucionado a tiempos de generación largos, lo que las hace especialmente vulnerables a la variabilidad ambiental (Louzao 2006). Además, aunque las aves marinas pasan la mayor parte del tiempo en el mar, vuelven regularmente a las zonas costeras para reproducirse, lo que las expone a un gran mosaico de perturbaciones, tanto marinas como terrestres (Schreiber and Burger 2001, Paleczny et al. 2015). También, son relativamente fáciles de estudiar y son consideradas especies banderas, por lo que están comparativamente mejor estudiadas que cualquier otro grupo de vertebrados (Schreiber and Burger 2001, Bennett and Owens 2002, Croxall et al. 2012, Paleczny et al. 2015). En resumen, las aves marinas son un modelo excelente para evaluar los efectos de la variabilidad ambiental y las perturbaciones en la dinámica de poblaciones porque están muy bien estudiadas, sus rasgos vitales las hacen vulnerables a numerosas perturbaciones y su ecología integra procesos a diferentes escalas espacio-temporales (Paleczny et al. 2015).

Esta tesis se centra en el estudio de las perturbaciones y la variabilidad ambiental en un grupo determinado de aves marinas, las gaviotas. De las aves marinas las gaviotas son uno de los grupos menos especializados y presentan particularidades en su ecología trófica, espacial y reproductora. Las gaviotas son especies generalistas, oportunistas y omnívoras que se alimentan de una gran variedad de recursos como por ejemplo insectos, calamares, crustáceos, moluscos, lombrices, pequeños mamíferos, semillas, frutos, basura o descartes pesqueros (Del Hoyo et al. 1996). A pesar de que muchas aves marinas tienen un bajo éxito reproductor, las gaviotas presentan un tamaño de puesta comparativamente alto, tres huevos (Del Hoyo et al. 1996). Las gaviotas tienden a moverse a regiones más cálidas durante el invierno. Sin embargo, por lo general cubren distancias más cortas que otras especies marinas como por ejemplo los Procelariformes (Del Hoyo et al. 1996). Como consecuencia, las gaviotas son consideradas especies nómadas en vez de migratorias (Del Hoyo et al. 1996). Por último las gaviotas comparten muchos hábitats con las poblaciones humanas, y como consecuencia de esta convivencia a menudo son consideradas como pestes (Del Hoyo et al. 1996). El interés social por controlar sus poblaciones ha resultado en la implementación de numerosos programas de control y en la producción de una extensa literatura científica sobre su biología. Por todo ello las gaviotas son un modelo especialmente prometedor para el estudio de las perturbaciones y la variabilidad ambiental en la dinámica de poblaciones (Sanz-Aguilar et al. 2009a,b).

Fuentes de alteración:

En la sección anterior comentábamos que las aves marinas se enfrentan a un amplio mosaico de amenazas terrestres y marinas. Las principales amenazas marinas a las que se enfrentan actualmente son las derivadas de su interacción con las pesquerías y la contaminación; mientras que en tierra son la presencia de depredadores invasores, la degradación del hábitat y las consecuencias de la actividad humana (Croxall et al. 2012). Como resultado, las aves marinas están más amenazadas que cualquier otro grupo de aves y su estado de conservación se ha deteriorado muy rápido en las últimas décadas (Croxall et al. 2012). A continuación explicaré como diferentes perturbaciones (objeto específico de la tesis pueden afectar la dinámica de poblaciones de las aves marinas. En particular, el cambio climático, los subsidios alimentarios o las interacciones intra- e inter- específicas. Las perturbaciones y fuentes de variabilidad descritas más abajo podrían causar tres efectos no excluyentes: las poblaciones de aves marinas podrían modificar su ecología trófica y reproductora para poder sobrevivir y reproducirse en la misma zona, modificar su distribución o morir (Gremillet and Boulinier 2009). Investigaciones recientes han revolucionado nuestra percepción de la ecología de las aves marinas y hay algunas evidencias que demuestran la capacidad de las aves marinas para tamponar la estocasticidad ambiental (Crawford 2009, Crawford et al. 2015). Sin embargo, la plasticidad fenotípica y comportamental puede estar limitada fisiológicamente y una vez superado un determinado umbral las poblaciones pueden no ser capaces de tolerar más cambios (Crawford et al. 2015).

Cambio climático

Los eventos extremos y cíclicos son una parte inherente de los sistemas naturales y las aves marinas han evolucionado en ambientes variables. Sin embargo, hay evidencias claras de que las actividades humanas son responsables del cambio global y de los incrementos en la estocasticidad ambiental (Alley et al. 2003, Halpern et al. 2008). A pesar de que existe incertidumbre sobre los efectos de dichos cambios, las respuestas ecológicas al cambio global ya son visibles (Walther et al. 2002). El cambio global a generado respuestas en la composición, estructura y dinámica de los ecosistemas, la distribución de especies/poblaciones y en la fenología y fisiología de los organismos (Walther et al. 2002). Por ejemplo, se han detectado reducciones significativas en la productividad primaria de determinadas zonas, con importantes consecuencias en la disponibilidad de alimento para los depredadores marinos (Hutchings et al. 2009, Lindegren et al. 2013). Procesos a larga escala como El Niño, la Oscilación del Atlántico Norte, las anomalías en la temperatura oceánica superficial y la cobertura de hielo en los casquetes polares han causado cambios en las áreas de forrajeo y causado grandes mortalidades y fallo reproductor en las aves marinas (Barbraud and Weimerskirch 2001, Stenseth et al. 2003, Jenouvrier et al. 2005). Además, hay evidencias de que el cambio climático puede tener efectos sinérgicos en las interacciones con otras perturbaciones naturales y antropogénicas aumentando la complejidad de las interacciones ecológicas (Walther et al. 2002, Gremillet and Boulinier 2009).

Subsidios alimentarios predecibles de origen antropogénico — PAFS

Los subsidios alimentarios predecibles de origen antropogénico tienen importantes consecuencias ecológicas y evolutivas (Oro et al. 2013a). Afectan a los ecosistemas alterando procesos como la competencia, las dinámicas de depredador–presa o los ciclos biogeoquímicos (Oro et al. 2013a). Los PAFS son muy predecibles espacio-temporalmente comparados con las fluctuaciones estocásticas inherentes a los sistemas naturales (Oro et al. 2013a). Una vez aparecen, causan la homogeneización del ambiente ya que reducen la variabilidad espaciotemporal de las poblaciones y aumentan la resiliencia de las especies oportunistas (Bicknell et al. 2013). A pesar de que la alta predictabilidad puede traducirse en mayor estabilidad, mayor estabilidad no necesariamente implica mayor resiliencia (Holling 1973). Las propabilidades de persistir pueden verse reducidas ya que las fluctuaciones poblacionales son esenciales para responder a las perturbaciones (Holling 1973). A nivel poblacional, la disponibilidad de una fuente de comida muy predecible en el espacio y en el tiempo causa efectos importantes en la estructura y dinámica poblacional dado que su presencia por lo general causa un aumento del éxito reproductor, de la supervivencia, del tamaño poblacional y genera cambios en la dispersión (Oro et al. 2013a).

Además, los PAFS pueden causar diferencias morfológicas y comportamentales entre poblaciones y éstas derivar en cambios en las frecuencias de diferentes genotípos (Yom-Tov 2003). Los dos subsidios alimentarios más importantes a nivel mundial son los vertederos y los descartes pesqueros (Oro et al. 2013a). Ciertas medidas han sido implementadas a nivel mundial para intentar reducir sus efectos. Por ejemplo, recientes modificaciones de la política pesquera o de la política de vertido de residuos intentan, respectivamente, reducir los descartes y acabar con los vertederos a cielo abierto (Parliament 2013, E.U. 2009, European-Commission 2008). Sin embargo, dichas medidas a pesar de intentar reducir las consecuencias de las perturbaciones humanas, pueden ser a su vez convertirse en una perturbación. Una pregunta interesante pero de difícil respuesta es desentrañar como las poblaciones responderán a cambios en la disponibilidad de PAFS (Oro et al. 2013a, Sarda et al. 2015).

Interacciones inter- e intra- especificas:

Depredación

La depredación es una fuente de heterogeneidad en la estructura y dinámica poblacional de las poblaciones silvestres; además, es un importante agente de selección en la evolución de las historias y rasgos de vida (Sousa 1984). La introducción de especies nativas y no nativas como consecuencia de las actividades humanas está directamente realccionada con la extinción y el declive de numerosas especies de aves marinas (McCreless et al. 2016). Las aves marinas han evolucionado en ambientes libres de depredadores, por lo tanto no cuentan con los mecanismos comportamentales adecuados para responder a la depredación y a menudo sufren efectos letales y subletales de la presencia de depredadores (Wanless et al. 2007). En ocasiones la depredación actúa eliminando de la población individuos que ya estaban condenados (mortalidad compensatoria) lo que en principio no tendría efecto sobre la densidad poblacional; sin embargo, en ocasiones también puede causar mortalidad aditiva y dar lugar a colapsos poblacionales. Los efectos no letales como las molestias o el estrés fisiológico pueden causar cambios en la distribución, abundancia e interacción de los individuos, dando lugar a cambios en la dinámica de poblaciones (May and McLean 2007). Son particularmente interesante las consecuencias de los diferentes efectos de la presencia de depredadores en los individuos dependiendo de sus rasgos como pueden ser la edad, el sexo o la experiencia. Dichos rasgos pueden afectar las dinámicas de poblaciones a largo plazo ya que pueden determinar la capacidad de las poblaciones para adaptarse a cambios ambientales (Teitelbaum et al. 2016).

Densodependencia

Otra cuestión crucial en el estudio de la dinámica de poblaciones son los efectos de la densodependencia en la regulación de las poblaciones y su interacción con la estocasticidad ambiental (Tujlapurkar and Caswell 1997, Coulson et al. 2001b, May and McLean 2007). La densodependencia puede surgir en poblaciones naturales como consecuencia de la interacción con otros miembros del sistema — por ejemplo en forma de competencia por recursos. Los efectos densodependientes son especialmente importantes después de periodos con condiciones ambientales favorables, bajo estas condiciones las poblaciones son susceptibles de aumentar y los efectos densodependientes, así como sus interacciones con eventos ambientales extremos, son más susceptibles de ocurrir (Coulson et al. 2001b). También es importante reconocer que aunque parezca que las poblaciones sigan dinámicas densoindependientes, es posible que estén sujetas a efectos desfasados y que esos respuestas desfasadas temporalmente tengan efectos desestabilizadores para la dinámica de poblaciones (Turchin 1990, May and McLean 2007). Entender y reconocer la importancia de las interacciones (no-lineales) entre las perturbaciones naturales y antrópicas es fundamental para desentrañar el funcionamiento de las poblaciones bajo distintos regímenes de perturbaciones.

Modelos y modelado: un marco metodológico general

El estudio de la dinámica de poblaciones es una empresa arriesgada. Primero por que requiere el uso de modelos complejos, así como una gran potencia computacional. Además requiere el mantenimiento del estudio a largo plazo de especies salvajes, lo que es tanto económica como logísticamente complicado. El objetivo principal de la ecología de poblaciones y en particular del modelado ecológico es intentar explicar lo que observamos en el campo. En cualquier caso, el marco teórico y las herramientas estadísticas que usamos para enfrentarnos a una pregunta en particular dependen directamente de nuestros objetivos (Tujlapurkar and Caswell 1997). En las secciones anteriores he intentado dar un marco teórico y un contexto ecológico a mi tesis. Ahora describiré las herramientas estadísticas que he seleccionado para responder a cada una de las hipótesis planteadas sobre el efecto de las perturbaciones y la variabilidad ambiental en la dinámica de poblaciones.

Me gustaría resaltar la importancia de las respuestas no lineares a las perturbaciones, a pesar de que mucha de la metodología empleada en esta tesis usa técnicas de linearización — una obvia simplificación de la realidad. Además, no intento describir en detalle cada una de las metodologías empleadas, lo cual ya he hecho en cada uno de los capítulos, sino dar una visión clara y simplificada de las diferentes metodologías.

Modelos de captura, recaptura y recuperación

Por lo general para estimar de manera robusta las densidades de población y las tasas de supervivencia y movimiento de una población es necesario capturar y marcar individuos para que puedan ser identificados en encuentros sucesivos (Lebreton et al. 1992). En esta tesis empleo la metodología de captura, recaptura y recuperación para estimar la abundancia poblacional y la probabilidad de supervivencia. He calculado la abundancia poblacional a través del método de Petersen-Lincoln y las estimas de supervivencia han sido producidas a través de modelos multiestado y multievento (Pradel 2005). Los modelos multiestado permiten la estima de la probabilidad de supervivencia y la probabilidad de transición entre estados (Kendall and Nichols 2002, Pradel et al. 2005, Conn and Cooch 2009). Los modelos multievento permiten, además, incorporar la incertidumbre del estado en el que se encuentran los individuos (Pradel 2005).

Análisis de isótopos estables

Los análisis de isótopos estables fueron usados originariamente,a finales de los años 70, para desentrañar el contenido de las dietas animales (DeNiro and Epstein 1978). Desde entonces se han producido grandes avances tanto en la instrumentación como en la interpretación de los procesos que causan variaciones en los ratios isotópicos de las diferentes sustancias (Forero et al. 2005, Caut et al. 2009, Ramos et al. 2009b). Su uso se ha generalizado y hoy son una herramienta muy popular que permite distinguir entre diferentes niveles tróficos, áreas de forrajeo y recursos (Hobson 1987, Forero et al. 2005, Caut et al. 2009).

De las regresiones lineales a los modelos lineales generalizados mixtos

Los modelos de regresion lineal permiten explorar la relación entre una variable dependiente y una variable explicativa junto con su generalización multivariante se han empleado extensamente en ecología y han permitido responder un gran número de preguntas. Sin embargo, los datos ecológicos rara vez cumplen las asunciones de normalidad que requieren estos modelos estadísticos (Bolker et al. 2009). Las desviaciones de esas asunciones no deberían evitar el uso y análisis de datos atípicos que pueden ser analizados con los modelos lineales generalizados mixtos (GLMMs). Los GLMMs combinan las propiedades de ambos marcos estadísticos — modelos lineales mixtos y modelos lineales generalizados — como resultado son una herramienta muy ponderosa para el análisis de datos no normales que cuentan con efecto aleatorios (Bolker et al. 2009).

Análisis de punto de corte

Por último, cuando analizamos los efectos de la variabilidad ambiental nos enfrentamos a retos que van más allá de la cuantificación de la relación de una o más variables. A menudo necesitamos identificar determinados umbrales que determinan el cambio de comportamiento de un sistema. Para suplir esa necesidad surgió el análisis de puntos de corte cuyo uso se ha generalizado en las dos últimas décadas.

Objetivo general y esquema de la tesis

El objetivo general de la tesis es explorar los efectos de la variabilidad ambiental y de las perturbaciones en la demografía de poblaciones de depredadores apicales marinos (gaviotas) a través de diferentes escalas espacio-temporales. Específicamente, exploro los efectos del clima, PAFS e interacciones biológicas como la densodependencia o la depredación. Esta tesis está estructurada en 4 capítulos principales (Capítulos 1-4), que son coherentes y abordan preguntas biológicas diferentes, y un capítulo final que resume las conclusiones de la tesis, discute los resultados y posibles mejoras. El documento cuenta con una lista general de referencias al final de la discusión general.

Abajo pueden encontrar un breve resumen de los objetivos particulares de cada uno de los 4 capítulos :

- En el capítulo 1 he evaluado las consecuencias de dos perturbaciones consecutivas — el fin de los subsidios alimentarios predecibles de origen antropogénico y un evento de mortalidad estocástica — en la ecología trófica, supervivencia y tamaño poblacional de una especie generalista de ave marina que por lo general es considerada una peste, la gaviota patiamarilla (*Larus michahellis*). Para lograr estos objetivos, primero estimé la composición y la variación temporal de la dieta mediante el uso de isótopos estables. Después, utilice modelos multiestado y datos de captura, recaptura y recuperación para estimar la supervivencia local y evaluar el potencial efecto a corto y largo plazo de las perturbaciones consecutivas. Por último, evalué posibles cambios en la tendencia poblacional.

- En el capítulo 2, exploramos los costes de las condiciones ambientales durante los primeros estadios de vida en una especie longeva de ave marina, la gaviota de

Audouin (*Ichthyaetus audouinii*). Específicamente, comprobamos los potenciales efectos cohorte de naturaleza maternal y carácter densodependiente y los efectos de las condiciones ambientales en las zonas de invernada durante el primer año de vida. En este caso, utilizamos datos una serie de datos de 26 años de captura, recaptura y recuperación de las gaviotas de Audouin que crían en el Delta del Ebro. Su análisis se realizó mediante modelos multievento ya que permitían incluir la incertidumbre sobre los estados no observados y la heterogeneidad de la recaptura. Este es el primer intento de modelizar los costes de supervivencia a corto y largo plazo como consecuencia de las condiciones durante dos periodos críticos de vida temprana, la fase de cría y el primer invierno.

- En el capítulo 3, examiné la dinámica de colonización de una especie longeva de ave marina, la gaviota de Audouin, durante las tres últimas décadas a lo largo de la costa Mediterránea. Al hacerlo, intento esclarecer algunos aspectos sobre la relación de las perturbaciones, las condiciones adversas de cría y las colonizaciones. En primer lugar, empleo análisis de cambio de fase que permiten identificar momentos de cambio en el proceso de colonización y encontrar potenciales relaciones cualitativas con las perturbaciones y condiciones adversas. En segundo lugar, evaluamos el papel de la información personal en los procesos de colonización. Por último evaluamos las consecuencias de las colonizaciones en la eficiencia ecológica.

- En el capítulo 4, he estudiado el papel de los efectos no letales de la presencia de depredadores en la persistencia de las poblaciones. He usado series de datos de captura- recaptura de 23 años de duración de la gaviota de Audouin para evaluar si las perturbaciones y la dispersión pueden llegar a comprometer la persistencia de las poblaciones. En particular, he cuantificado los cambios en la estructura de edad, el rendimiento reproductor (volumen de huevo, tamaño de puesta y éxito reproductor) y la reubicación de las áreas de cría en la colonia del Delta del Ebro.

II | Main chapters

1

Population control of an overabundant species achieved through consecutive anthropogenic perturbations

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Data is deposited in the CEDAI Repository:
M ARRAY *Larus michahellis* Dragonera
<http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=c867ca26-7b03-4dcb-ac26-7ef0ab536762>
Stable Isotope Signature *Larus michahellis* Dragonera
<http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=280c2ad4-5204-4dde-b703-2ece5625730f>
Nest abundance *Larus michahellis* Dragonera 2008 2013
<http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=be15329b-5f71-4b9c-bd02-5cddcb67a553>

1.1 Abstract

The control of overabundant vertebrates is often problematic. Much work has focused on population-level responses and overabundance due to anthropogenic subsidies. However, far less work has been directed at investigating responses following the removal of subsidies. We investigate the consequences of two consecutive perturbations — closure of a landfill and an inadvertent poisoning event — on the trophic ecology ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), survival, and population size of an overabundant generalist seabird species, the yellow-legged gull. We expected that the landfill closure would cause a strong dietary shift and the inadvertent poisoning a decrease in gull population size. As a long-lived species, we also anticipated adult survival to be buffered against the decrease in food availability but not against the inadvertent poisoning event. Stable isotope analysis confirmed the dietary shift towards marine resources after the disappearance of the landfill. Although the survival model was inconclusive, it did suggest that the perturbations had a negative effect on survival, which was followed by a recovery back to average values. Food limitation likely triggered dispersal to other populations, while poisoning may have increased mortality; these two processes were likely responsible for the large fall in population size that occurred after the two consecutive perturbations. Life-history theory suggests that perturbations may encourage species to halt existing breeding investment in order to ensure future survival. However, under strong perturbation pulses the resilience threshold might be surpassed and changes in population density can arise. Consecutive perturbations may effectively manage overabundant species.

Key-words: Food availability, predictable anthropogenic food subsidies, seabird, population size, adult survival, pest, stable isotope analysis, anthropogenic perturbation.

1.2 Introduction

Human alterations of natural systems have triggered profound changes in ecosystem functioning and species communities (Vitousek et al. 1997). For instance, predictable anthropogenic food subsidies, such as landfill organic waste, have caused ecological and evolutionary changes at individual, population, community and ecosystem levels (Oro et al. (2013a) and references therein). Exploitation of subsidies alters not only dietary preferences but may increase body mass, body size, breeding performance or survival on a wide range of species (Newsome et al. 2015). Subsidies are considered responsible for much of the demographic explosion of a wide range of so-called 'overabundant' species such as foxes, gulls and rats (Duhem et al. 2008, Bino et al. 2010, Aplin et al. 2011). A large number of studies have tackled mitigation and management measures, such as direct culling aimed at reducing the ecological and social consequences of overabundant species (Baker and Harris 2006, Beasley et al. 2013, Bosch et al. 2000, Merrill et al. 2006). However, although these measures have been implemented worldwide, they have often turned out to be expensive and/or ineffective (Baker and Harris 2006, Oro and Martínez-Abraín 2007, Warburton and Norton 2009). The main flaw is that management measures often aim to mitigate the consequences of the human alteration rather than avert the occurrence of the alteration itself.

However, recent European Union (EU) environmental policies are beginning to target the causes rather than their 'symptoms' For example, the final modifications to the Landfill Waste Council Directive (LWCD; E.U. (2009), European-Commission (2008))aim to put an end to open-air landfill sites. In addition, these policies target a progressive reduction of predictable subsidies and are expected to trigger population control in some overabundant species. The exhaustive monitoring of the ecological processes ensuing after the closure of open-air landfill sites provides a unique perspective and understanding of the consequences to ecosystems of a forced reduction in supplementary feeding (Steigerwald et al. 2015). Since seabirds are easily monitored and sensitive to changes in food availability, they provide a particularly good model for understanding the complexity and the efficacy of recent policy changes aimed at controlling overabundant species. For instance, changes caused by food limitation have been previously documented for seabird clutch size, egg volume, body size, breeding success, fecundity, adult survival, local recruitment, dispersal and population size (Pons and Migot 1995, Harris et al. 1997, Oro and Furness 2002, Duhem et al. 2008, Oro and Pradel 2000)

Predictable food subsidies together with the protection of suitable breeding areas in recent years has led to an increase in large opportunistic gull populations (Duhem et al. 2008). Their growth has caused social annoyance as well as concerns for public health (Hatch 1996), and have trigged population control measures worldwide (Thomas 1972, Vidal et al. 1998, Bosch et al. 2000, Brooks and Lebreton 2001).

For instance, yellow-legged gulls *Larus michahellis* (YLG hereafter) in the Mediterranean basin have been subject to numerous culling programs aimed at controlling their numbers — the 'symptom' — by targeting either a reduction in adult survival rates or breeding performance (Vidal et al. 1998, Brooks and Lebreton 2001, Duhem et al. 2008). Because seabirds are long-lived species, the reduction of adult survival is expected to have important population consequences (Saether et al. 1996). However, direct culling had little effect on gull numbers because processes such as earlier recruitment or density-dependent higher fertility and immigration (Brooks and Lebreton 2001) were likely enhanced by high food availability, which might have boosted gulls' resilience to this type of perturbation (Oro and Martínez-Abraín 2007). Although food limitation has some impact on breeding performance, it is not expected to be particularly useful in controlling long-lived species; nevertheless, a long-term limitation of resources might be the key to controlling overabundant species by reducing recruitment (Oro and Martínez-Abraín 2007). When the two types of measures (food limitation and culling) are used together, their synergic or cumulative effects may lead to an important reduction in population size, although very little is known about the potential effects of linked management actions.

YLG are large, colonial and opportunistic seabirds distributed over the whole Mediterranean basin. YLG are known to exploit landfills to varying extents throughout their distribution range (Witt et al. 1981, Motis 1989, Bosch et al. 1994, Verdu del Campo et al. 1995, Ramos et al. 2009a). Particularly, Ramos et al. (2011) assessed the importance of landfills on YLG in the Western Mediterranean basin, and demonstrated that landfill waste represents up to 60‰of the diet of breeding YLG in our study colony. The recent explosion in YLG numbers has raised conservation concerns and several culling programs have been carried out in different locations. Despite these control measures, it is still the most abundant seabird in the Mediterranean (Zotier et al. 1999, Oro and Martínez-Abraín 2007).

We assessed 1) the consequences on the ecology of YLG of two anthropogenic perturbations, the closure of an open-air landfill site due to European Directives (E.U. 2009), which was estimated to represent half of its diet in terms of assimilated biomass (Ramos et al. 2011); and 2) the use of poison pellets in the study area to eradicate invasive pest, which caused indirect mortality in YLG from primary (ingestion of pellets) and secondary (ingestion of poisoned rodents) poisoning (Mayol et al. 2012a). We investigated the changes in trophic ecology (dietary shift) and demographic parameters (population size and survival) of breeding YLG's that were attributable to the two consecutive anthropogenic perturbations. Life-history theory predicts that under limited food access, long-lived organisms will forego reproduction to avoid negatively affecting their future survival (Pugesek and Diem 1990, Oro et al. 1999). Thus, we expected that food limitation would trigger a dietary shift and differential resource exploitation, affecting breeding performance (Oro et al. 1995, Steigerwald et al. 2015) but not individual survival probability. Moreover, we expected that the inadvertent poisoning event would cause an increase in mortality rate due to the accidental poisoning of individuals. We expect that the combined effects of one action affecting reproductive performance and another affecting adult survival might trigger a decrease in population size. In addition, we expected our results to shed more light on the effects of consecutive perturbations and to provide a more comprehensive framework for superabundant species management.

1.3 Material and methods

1.3.1 Study area and perturbations

Data were collected at Dragonera Natural Reserve, a 300 ha island off the coast of Majorca (Balearic archipelago, Spain, 39°35′02″N, 02°19′17″E). This protected site hosts the largest-known YLG breeding colony in the archipelago (McMinn 2010). YLG nests can be found all over the island, with areas of gentle slope and low vegetation having higher density. The tourism industry on Majorca (ca. 10^7 tourists/year with a population of ca.

10^6 residents) has increased waste production and its availability at a single landfill site for opportunistic feeders. This anthropogenic subsidy was responsible for the doubling of the YLG Balearic archipelago population between 1983 (ca. 7500 pairs) and 2000 (ca.14000pairs; McMinn (2010)). Local managers estimated the number of gulls foraging at the landfill (ca. 32km from Dragonera) to range between 7300 and 15500 depending on the season and the year (TIRME 2003). Following European Directives (E.U. 2009), the open-air landfill was transformed into an incineration plant in the winter $2009-2010$. This transformation made waste virtually inaccessible to gulls. In mid winter of the year after the transformation (January and February 2011), an eradication campaign targeting the human-introduced rats (*Rattus rattus*), mice (*Mus musculus*) and rabbits (*Oryctolagus cuniculus*) was carried out on Dragonera (Mayol et al. 2012b). This campaign involved the aerial application of Brodifacoum, a second generation anticoagulant whose main mechanism is blocking epoxy-reductose enzyme activity. Without generating bait shyness, this leads to lack of blood clotting factors, followed by hemorrhages and eventually death (Hadler and Buckle 1992). In the weeks following the spread of the poison, ca. 800 YLG carcasses were found on the island (de Proteccio d'especies 2011). This can be considered a minimum estimate given that the search was not exhaustive and the areas with dense vegetation and surrounding waters were not surveyed (de Proteccio d'especies 2011).

1.3.2 Trophic level and dietary shift

Nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and sulphur ($\delta^{34}S$) isotopic ratios can be used in ecological studies to evaluate dietary shifts (Ramos et al. 2011), since analyses of individual feathers provide unique isotopic information for very specific spatiotemporal periods (Hobson 2008). We evaluated the nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and sulphur ($\delta^{34}S$) isotopic ratios of the first primary feather (P_1) on 68 unique breeding YLG individuals captured (see below) in 2004 ($N = 12$), 2008 ($N = 18$), 2011 ($N = 18$) and 2013 ($N = 20$) (Table 4). P_1 feathers were collected during the incubation period (April-May). Feathers were removed by cutting the feather quill, which causes no damage to the individuals. The P_1 feather is replaced by molt at breeding sites and its isotopic value is an indicator of the diet of the previous breeding season.

Laboratory procedures for preparing and processing feather samples were carried out following Ramos et al. (2011). Feathers were washed in a 0.25 m sodium hydroxide solution, rinsed thoroughly in distilled water to remove any surface contaminants, dried in an oven at 60°C to constant mass and ground to a fine powder in a freezer mill (Spex Certiprep 6750; Spex Industries Inc., Metuchen, NJ, USA) operating at liquid nitrogen temperature. Subsamples of powdered material were weighed to the nearest μ g, placed in tin capsules and crimped for combustion for C, N and S isotope determination.

Isotopic analyses were carried out at the Serveis Científico-Tècnics of the University of Barcelona (Spain) by means of a Thermo-Finnigan Flash 1112 (for N and C)/1108 (for S)(CE Elantech, Lakewood, NJ, USA) elemental analyzer coupled to a Delta-C isotope-ratio mass spectrometer via a CONFLOIII interface (Thermo Finnigan MAT, Bremen, Germany), and applying IAEA standards (IAEA CH6, IAEA CH7 and USGS 24 for C, IAEA N1, IAEA N2 and IAEA NO3 for N, and IAEA-S1, IAEA-S2 and IAEA-S3 for S) every 12 samples to calibrate the system and compensate for any drift over time. Samples from 2004 were analyzed separately from 2008, 2011 and 2013 but the same instruments and standards were used. Precision and accuracy for $\delta^{13}C$ measurements was ≤ 0.1%¸, ≤ 0.3%¸ for $\delta^{15}N$ and ≤ 0.3%¸ for $\delta^{34}S$. Results were expressed in delta (δ) notation (Bond and Hobson 2012).

We used linear mixed models (LMM) to evaluate the effects of landfill closure, sex and their interaction (Crawley 2007), with the year as the random effect (Zuur et al. 2009), to account for the effect of environmental variability on isotopic signatures. In addition, we estimated diet composition before and after landfill closure for males and females by applying Bayesian three-isotope ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values), three-endpoint (marine, crops and terrestrial environments, and refuse sites) mixing models to the isotopic values (SIAR, Stable Isotope Analysis in R; Parnell et al. (2008) . Ramos et al. (2011) recently evaluated the spatiotemporal variations the feeding ecology of YLG on the western Mediterranean region. Prey isotopic signatures were homogeneous among most of the localities studied, hence we included mean isotopic values ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) calculated in their study for the main food resources exploited by YLG in Dragonera (values from Table 5 in Ramos et al. (2011) Ramos et al 2011). Moreover, we used the consumer-discrimination factors provided by these authors.

1.3.3 Local survival analysis and estimates of population abundance

Breeding adults were trapped during the incubation period using a tent spring trap (see Steigerwald et al. (2015). We chose to trap individuals in accessible nests along the main south path of the island (4.5 Km long) to increase resighting probabilities in the following years. In total we trapped 206 YLG, which were marked using a Darvic plastic band with a unique alphanumeric code for subsequent individual identification from a distance using spotting scopes. Marking, resighting of live birds, and recovery of dead animals (99 and 12 cases respectively) in March/April in 2007–2013 were used to build individual encounter histories and analyzed using multistate capture-mark-recapture-recovery (CMRR) models to estimate survival, recapture and recovery probabilities (Brownie et al. 1993, Lebreton et al. 1999). Since all recoveries came from the colony site, CMRR models cannot distinguish mortality from permanent emigration to unobservable areas of the island. As a consequence, our estimates refer to apparent survival (Lebreton et al. 1999).

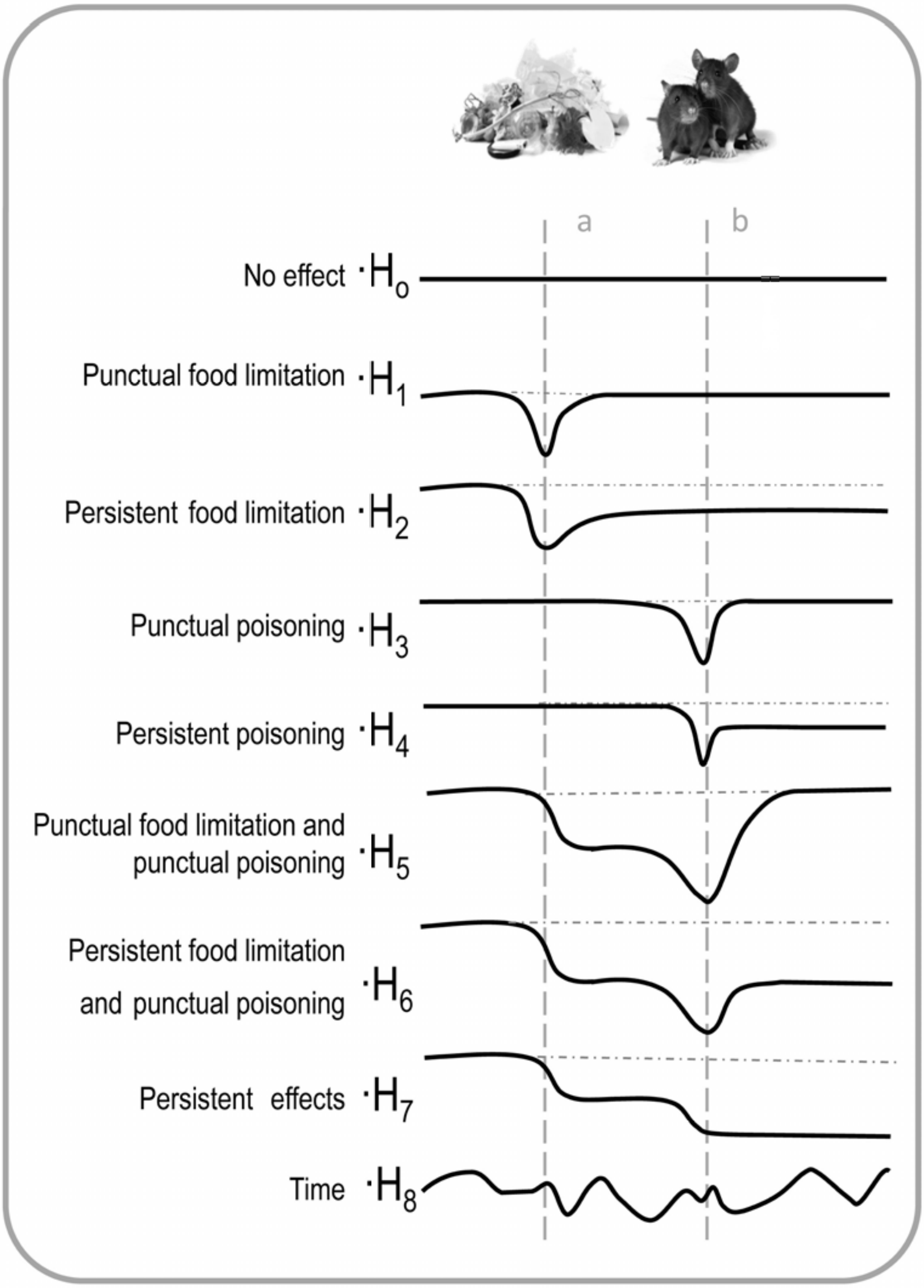

Fig. 1: Survival probability (ϕ): qualitative representation under different biological hypotheses. Dashed lines 'a' and 'b' represent the landfill closure and the eradication campaign respectively. Survival hypotheses are numbered in growing complexity and assigned to the analogous model on Table 6 (model number in brackets): $H_0(M_0)$, $H_1(M_1)$, $H_2(M_2)$, $H_3(M_3)$, $H_4(M_4)$, $H_5(M_5)$, $H_6(M_6)$, H_7 (M_7) and $H_8(M_8)$.

We assessed the goodness-of-fit test (GoF) for the general model assuming that all parameters vary over time (Jolly-Move model; Brownie et al. (1993), Pradel et al. (2003) using the software U-CARE 2.2.2 (Choquet et al. 2005, 2009). The global GoF test revealed no evidence of transient animals, meaning that there was no difference in the probability of being later reencountered between 'new' and 'old' individuals encountered at a given time, and that there were no trap-dependence effect (i.e., no difference in the probabilities of being reencountered in the different stages at $i+1$ between the animals in the same state at occasion i whether or not encountered at this date).

Thus, the general model adequately explained the data ($\chi^2 = 37.483$, $df = 35$, $P-value = 0.356$; Table ??). The GoF test for females indicated the presence of transients, but since the global GoF was not statistically significant we used a variance inflation factor, $\hat{c} = 1.07$, to account for the remaining heterogeneity (Choquet et al. 2005, 2009). We identified a set of biological hypotheses (Fig. 1). and began by testing effects on a single parameter at a time (Lebreton et al. 1992).

Table 3: Goodness of fit tests for Yellow Legged gulls breeding at Dragonera Island

Males	Test	χ^2	df	p-value	$\hat{c}$
	3G.SR	2.90	5	0.72	0.58
	3G.SM	1.66	4	0.80	0.41
	M. Itec	3.54	5	0.62	0.71
	M. Ltec	0.37	3	0.95	0.12
	Global 3G	4.55	9	0.87	0.51
	Global M	3.91	8	0.87	0.49

Females	Test	χ^2	df	p-value	$\hat{c}$
	3G.SR	16.02	5	0.01	3.20
	3G.SM	4.18	4	0.38	1.05
	M. Itec	3.16	5	0.68	0.63
	M. Ltec	5.62	4	0.23	1.41
	Global 3G	20.20	9	0.02	2.25
	Global M	8.82	9	0.45	0.98

Results of the goodness of fit (GoF) tests for the general capture–recapture-recovery multistate (CMRR) model for males and females YLG. Test components are listed as in (Pradel et al. 2003) where 3G: Tests for transients presence and M. Tests for trap dependence;χ^2: χ^2 statistic; df: degrees of freedom; $\hat{c}$:inflation factor i.e., χ/df.

We considered the effect of year, sex, landfill closure and the pest eradication campaign on local survival probability (Fig.1).The landfill closure and pest eradication campaign effects were tested either as punctual or persistent depending on the temporal extent (short *vs.* long term, respectively) of the effect in the considered hypothesis (Fig. 1). Furthermore, we used the number of days spent searching for marked animals as a predictor of recapture probability and the effort (number of searching days) invested in searching for corpses by the Dragonera Natural Reserve team as a predictor of the recovery rate. We began by simplifying the structure of the recovery rate (λ) from a general model (M_0), assuming all three parameters to be dependent on time and sex. We then modeled recapture (p) and finally the survival parameter (ϕ). Note that models' rank did not change when the model selection began with a different parameter (results not shown). Models were implemented using the program MARK 7.1 (White and Burnham 1999). Models were selected using the second order Akaike Information Criterion AIC_c value and, in addition, deviances were scaled using the over-dispersion dispersion parameter ($QAIC_c$; Burnham and Anderson (2002)). We considered the model with lowest AIC_c or $QAIC_c$ and those within two points of ΔAIC_c or $\Delta QAIC_c$ (the difference in AIC_c and $QAIC_c$ values, respectively) to be equivalent, and we used these models to produce final model-averaged parameter estimates ($Mean \pm SE$, Burnham and Anderson (2002). In this way we included the effects of parameters obtained from separate models and accounted for model selection uncertainty (Burnham and Anderson 1998). Each year, we estimated nest density in a 0.32 ha area (0.11% of Dragonera Island surface) with gentle slope and low vegetation as proxy of population size and for assessing its fluctuations over the study period. We assumed that despite that nest density might not be homogeneous within the island, the relative change in its value was a good indicator of population changes, as the surface occupied by the colony remained invariant. Five to nine observers walked the delimited area forming a transect line with a distance of ca. $3-5$m between each other and marking all encountered nests. Observers shuffled position within the line and surveyed the transect a second time to re-capture marked nests and count new ones. The number of nests in the area was then estimated by the Lincoln-Petersen estimator (Williams et al. 2001, Seber 2002). We used the *'delta method'* (Morgan 2000) to approximate the variance of the mean before and after the landfill closure and the pest eradication campaign. We then assessed if there was a population change after the events with a Z-test (Zar 2010).

1.4 Results

1.4.1 Trophic level and dietary shift

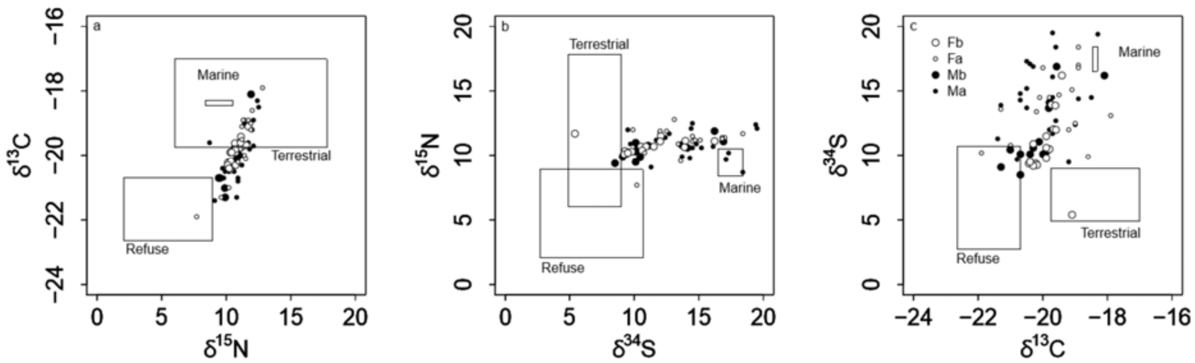

Fig. 2: Isotope signatures (‰) of $\delta^{13}C$ (a), $\delta^{34}S$ (b) and $\delta^{15}N$ (c) of male (solid circles) and female (open circles) yellow-legged gulls breeding on Dragonera Island before (large circles) and after (small circles) the landfill closure. Tissue: P_1 Feathers. Rectangles represent mean ±1.96 SE isotopic signature from marine, crops and terrestrial, and waste food sources, as calculated by Ramos et al. (2011).

We analyzed nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and sulphur ($\delta^{34}S$) isotopic ratios before and after the landfill closure (Table 4).

Table 4: Stable isotopic ratios before and after the landfill closure.

Male	Before	After
$\delta^{15}N$	10.69 ± 0.12	11.11 ±0.29
$\delta^{13}C$	-19.91 ± 0.10	-19.64 ±0.27
$\delta^{34}S$	10.85 ± 0.62	13.95 ±0.63

Female	Before	After
$\delta^{15}N$	10.50 ± 0.18	10.91 ± 0.22
$\delta^{13}C$	-20.13 ± 0.21	-19.94 ± 0.18
$\delta^{34}S$	11.48 ± 0.71	14.51 ± 0.60

Mean values ($\pm SE$) of nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and sulphur ($\delta^{34}S$) stable isotopes signatures (‰) of male and female Yellow legged gulls at Dragonera Island before (2004 and 2008) and after (2011 and 2013) the landfill closure.

The model selection procedure showed no significant changes in $\delta^{13}C$ before and after the landfill closure (Table 5, model M_1, see Appendix A.1 Table 10 for estimates). The landfill effect was not retained in the analysis of ($\delta^{15}N$,nTable 5, M_1, Appendix A.1 Table 10 for estimates), although that effect was present in an equivalent model ($\Delta AIC_c = 0.36$ for model M_2; Table 5, Appendix A.1, Table 10 for estimates). All retained models for $\delta^{34}S$ (Table 5, M_2, M_4 and M_5, see Appendix A.1: Table 10 for estimates) included the landfill effect as important, giving larger $\delta^{34}S$ values after landfill closure. Males and females had the same isotopic signature, however a sex effect was accounted for in two of the best three models of $\delta^{34}S$ (Table 4, M_4 and M_5, see Appendix A.1: Table 10 for estimates), indicating a small (not statistically significant) difference in male and female diet.

Table 5: Summary of model selection for isotope signatures of YLG breeding in Dragonera Island.

	Model notation	np	AIC_c	ΔAIC_c	W
$\delta^{13}C$					
M_1	$\delta^{13}C$	**1**	**170.40**	**0.00**	**0.58**
M_2	$\delta^{13}C_{LANDFILL}$	2	173.20	2.75	0.15
M_3	$\delta^{13}C_{SEX}$	2	172.60	2.19	0.20
M_4	$\delta^{13}C_{LANDFILL+SEX}$	3	175.10	4.65	0.06
M_5	$\delta^{13}C_{LANDFILL+SEX+LANDFILL*SEX}$	4	177.50	7.01	0.02
$\delta^{15}N$					
M_1	$\delta^{15}N$	1	187.40	0.00	0.43
M_2	$\delta^{15}N_{LANDFILL}$	2	187.70	0.36	0.36
M_3	$\delta^{15}N_{SEX}$	2	190.40	2.98	0.10
M_4	$\delta^{15}N_{LANDFILL+SEX}$	3	190.50	3.11	0.09
M_5	$\delta^{15}N_{LANDFILL+SEX+LANDFILL*SEX}$	4	192.60	5.27	0.03
$\delta^{34}S$					
M_2	$\delta^{34}S_{LANDFILL}$	2	321.70	0.00	0.33
M_4	$\delta^{34}S_{LANDFILL+SEX}$	3	322.00	0.35	0.28
M_5	$\delta^{34}S_{LANDFILL+SEX+LANDFILL*SEX}$	4	322.10	0.39	0.28
M_1	$\delta^{34}S$	1	325.20	3.54	0.06
M_3	$\delta^{34}S_{SEX}$	2	325.40	3.69	0.05

LANDFILL: landfill closure effect; SEX: sex effect; '+': additive effect; '$*$': interaction effect; AIC_c: corrected Akaike's information criterion; ΔAIC_c: AIC_c difference with the best model; w: weight. Best model in bold. All models include year as random factor.

Model results for isotopic contents (Table 5 and Fig. 2), together with the estimated percentage of diet diversity indicated by the SIAR analysis (Fig.3), revealed changes in resource use after the landfill closure: the marine content of the diet increased while refuse diet content decreased, as expected.

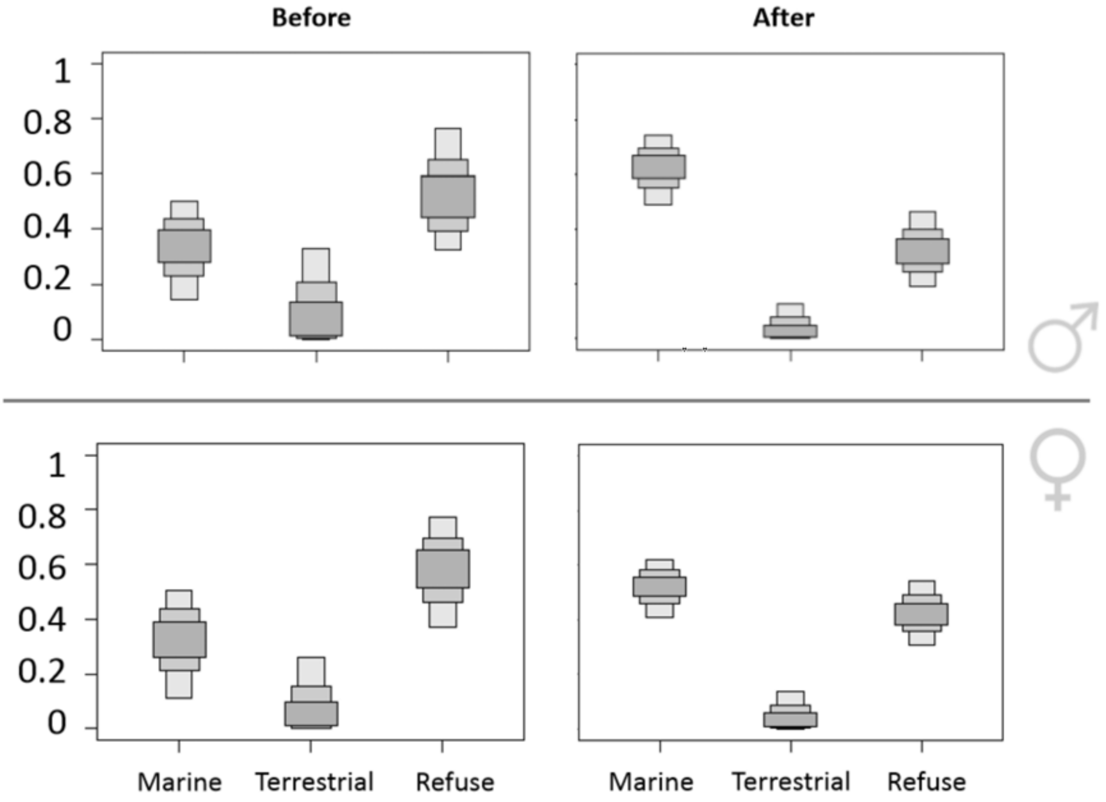

Fig. 3: Diet estimates of marine, terrestrial and waste resources (true proportions and their Bayesian credibility intervals including 50, 75 and 95% of the posterior distributions) estimated by Stable Isotope Analysis in R mixing modeling based on C, N and S isotopic signatures from the first primary (P_1) feathers of YLG from Dragonera Island before (left) and after (right) landfill closure, in males (upper panel) and females (lower panel). Sample sizes for males before landfill closure $N = 23$, males after $N = 9$, females before $N = 25$, and females after $N = 15$.

1.4.2 Local survival and population size

The model selection procedure resulted in five models having more than 10% of the $QAIC_c$ weight and occurring within 1 point of $QAIC_c$ value (Table 6), impairing conclusions on the statistical significance of each single effect. This uncertainty was probably due to the complexity of the model used to join two types of information (recoveries and recaptures) and the relatively small dataset available. Nevertheless, model averaging techniques took this uncertainty into account and delivered weighted estimates of the parameters of interest according to the model $QAIC_c$ value. The model with the lowest $QAIC_c$ value (model M_0, Table 6) indicated a constant survival, i.e. independent of sex and the perturbations or the years considered.

Averaged estimates were calculated for models M_{0-3} and M_5, which were within 2 $QAIC_c$ points of the one with the lowest value (M_0). All these models included the effect of food limitation and averaged estimates suggest that the closure of the landfill caused an 8% drop in survival (from 0.71 in 2009, $SE = 0.07$ to 0.63 in 2010, $SE = 0.07$). Similarly, the averaged estimates immediately after the pest eradication program

Table 6: Modelling of survival (ϕ), recapture (p) and recovery (λ) probabilities of yellow-legged gulls on Dragonera Island.

	Model notation	NP	$QAIC_c$	$\Delta QAIC_c$	W
M_0	$\phi_{.}p_E\lambda_B$	5	579.26	0.00	0.23
M_1	$\phi_{LANDFILL!}p_E\lambda_B$	6	579.76	0.50	0.18
M_3	$\phi_{PEST!}p_E\lambda_B$	6	580.17	0.91	0.15
M_2	$\phi_{LANDFILL\infty}p_E\lambda_B$	6	580.18	0.92	0.15
M_5	$\phi_{LANDFILL!+PEST!}p_E\lambda_B$	7	580.21	0.95	0.14
M_6	$\phi_{LANDFILL\infty+PEST!}p_E\lambda_B$	7	581.82	2.56	0.06
M_7	$\phi_{LANDFILL\infty+PEST\infty}p_E\lambda_B$	8	582.34	3.08	0.05
M_4	$\phi_{PEST\infty}p_E\lambda_B$	6	584.38	5.11	0.02
M_8	$\phi_T p_E\lambda_B$	10	584.88	5.62	0.01
M_9	$\phi_{T+SEX}p_E\lambda_B$	15	592.48	13.21	0.00
M_{10}	$\phi_{T+SEX}p_T\lambda$	20	595.99	16.73	0.00
M_{11}	$\phi_{T+SEX}p_{T+SEX}\lambda_B$	26	608.36	29.10	0.00
M_{12}	$\phi_{T+SEX}p_{T+SEX}\lambda_{B+SEX}$	28	612.40	33.14	0.00
M_{13}	$\phi_{T+SEX}p_{T+SEX}\lambda_{T+SEX}$	32	617.66	38.40	0.00

LANDFILL: landfill effect; T: year effect; B: recovery effort; E: recapture effort; PEST: Pest eradication effect; 'punctual: punctual; 'persistent': persistent; 'noeffect': no effect; 'additive': additional effect; NP: number of estimable parameters in the model; $QAIC_c$: Akaike's information criterion corrected for sample size, number of parameters and over-dispersion; $\Delta QAIC_c$: $QAIC_c$ difference with the best model; W: weight of the model. Best model in bold. Model subscripts refer to hypotheses in Fig.1.

indicated an additional 2% drop in apparent survival (from 0.63, $SE = 0.07$ in 2010 to 0.61, $SE = 0.11$ in 2011). The two synergic perturbations caused a 10% drop in survival probability when compared to the value before the landfill closure. We found no significant differences in either survival between males and females, or over time (Table 6, M_8-M_{13}. The search for carcasses and the sampling effort (Table 6, M_9 and M_{12}, respectively) well predicted recovery and recapture probabilities, respectively. Average recapture probabilities ranged between 0.24 ($SE = 0.06$) and 0.47 ($SE = 0.07$) (Fig 4 b), while recovery probabilities were constant (0.07, $SE = 0.03$), except for a 0.18 ($SE = 0.09$) increase in 2010 when a specific search for carcasses was conducted (Fig 4 c).

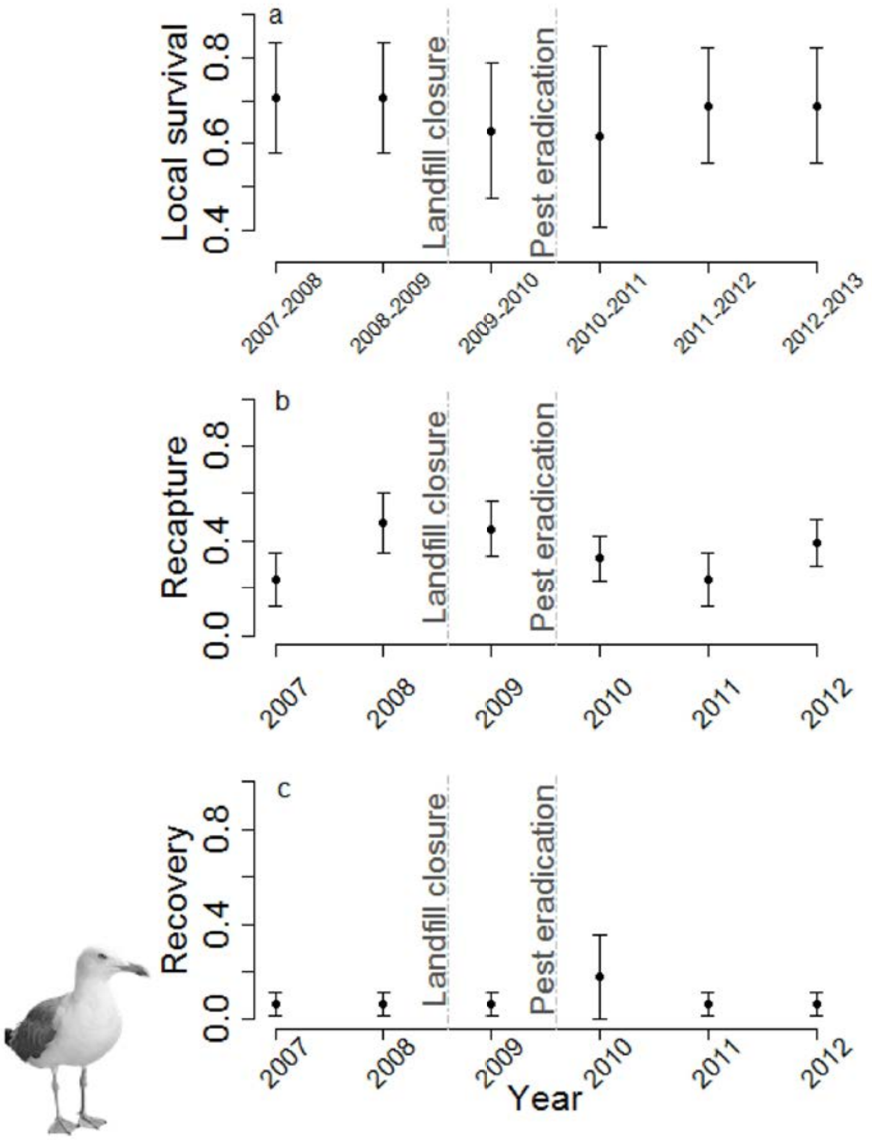

Fig. 4: Temporal variability in the estimated probabilities of local survival (a), recapture (b) and recovery (c) (95 ‰CI) of Yellow-legged gulls on Dragonera Island in 2007–2013 as estimated by the model averaging of the five best equivalent models with $\Delta QAIC_c < 2$ (Table 6).

Nest survey data clearly showed a decrease in size of the nesting population after the two perturbations (Fig.5). The number of nests in the surveyed area first decreased by 37% after the landfill closure (from 92.13 in 2009, $SE = 4.01$ to 58.05 in 2010, $SE = 5.71$), and had an additional drop of 65.99% after the pest eradication campaign (from 58.05 in 2010, $SE = 5.71$ to 20.19 in 2010, $SE = 2.30$; Fig. 5). Both perturbations caused a statistically significant change in nesting population size ($Z = 13.78$, $P < 0.00001$ and $Z = 17.19$, $P < 0.00001$ for landfill closure and poisoning campaign, respectively). The two synergic perturbations caused a 78% drop in nesting population size when compared to the value before the landfill closure (Fig. 5).

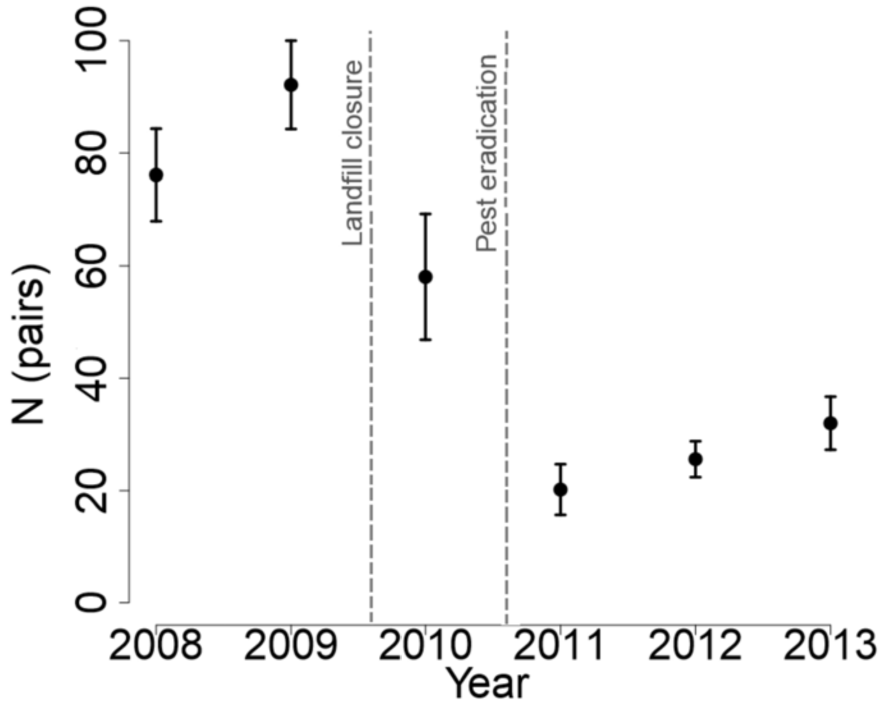

Fig. 5: Changes in nest density as a proxy of population size ($Mean \pm 1.96 SE$) of Yellow-legged gulls breeding on Dragonera Island. Dashed lines indicate landfill closure and pest eradication campaign.

1.5 Discussion

We assessed trophic and demographic changes in YLG after two consecutive anthropogenic perturbations, namely a food reduction after the closure of an open-air landfill and the accidental poisoning due to a campaign targeting the eradication of invasive mammals. Extensive research has been performed on the effects of predictable anthropogenic food sources across taxa (see reviews in Oro et al. (2013a) and Newsome et al. (2015)). Specifically, several studies on gulls have assessed the effects of food availability on several parameters such as diet (Ramos et al. 2011), survival (Oro et al. 1999) and population size (Oro et al. 1999, 2004, Duhem et al. 2008). These studies recorded that a decrease in the availability of food subsidies caused changes in resource exploitation and increased dispersal, whereas survival remained constant. However, none of these studies analyzed all these parameters simultaneously, nor did they evaluate the consequences of the combined effect of food limitation and additive mortality on population dynamics.

Predictable anthropogenic food can be a low-quality resource (the so-called 'junk-food', see Pierotti and Annett (1991), Annett and Pierotti (1999), Gremillet et al. (2008) and Genovart et al. (2010)) but gulls appear to adjust their diet in accordance with the availability, rather than with the quality, of foraging resources except when feeding chicks (Pons 1992, Pedrocchi et al. 1996, Oro et al. 2004). During the last few decades, landfills have provided YLG with a vast food surplus, leading to higher carrying capacity and rapid population growth (Duhem et al. 2008). It is likely that when access to this food was restrained, gulls were forced to exploit more energetically demanding and less predictable (unless obtained from fishery discards) marine prey (Bartumeus et al. 2010). Here we present partial evidence of this dietary shift towards marine resources in YLG trophic behavior following a landfill closure.

Since we were only interested in changes occurring at a population level, we did not account for the differences between individuals trophic behavior (Navarro et al. 2010). The evidence was clear in sulphur isotope signature: YLG exploited significantly more marine resources after the landfill closure; however, we failed to detect a change in carbon isotope signature. The threshold to detect a change in sulphur isotope signatures lies around 10‰while it is 3‰for carbon isotope signatures (see Figure 2 and mean isotopic values in Ramos et al. (2011). We attribute our non-statistically significant difference in carbon isotope signatures to a lack of statistical power, and hence cannot ascertain nor deny a possible effect. However, other YLG colonies have been observed to follow the same pattern (see Arizaga et al. (2013)). The use of $\delta^{34}S$ is commonly used to characterize the effect of marine food sources on various species (Lott et al. 2003, Natsumeda et al. 2015). Moreover, Moreno et al. (2010) demonstrated the potential of using $\delta^{34}S$ alone to distinguish not only between terrestrial and marine prey, but also between different marine prey species. Pedro et al. (2013) showed that exploitation of waste food by large, opportunistic gulls is a relatively new strategy that appeared less than 100 years ago. It is therefore not surprising that YLG from Dragonera were able to increase their consumption of marine and other terrestrial prey after food from landfill waste became unavailable. Moreover, other studies have also demonstrated a reduction in YLG waste consumption in this study area after the landfill closure (Ramos et al. 2011). It therefore seems reasonable to conclude that a diet change towards a marine diet occurred as a result of the landfill closure. Low food availability is also known to increase intraspecific competition and reduce the contribution of each individual to the next generation (Begon et al. 1996). Breeding seabirds suffering from food limitation face survival versus reproduction trade-offs, and they are expected to forego current reproduction to guarantee adult survival prospects in order to increase the odds of future generations living under favorable conditions (Pons 1992, Pons and Migot 1995, Oro et al. 1999, Sanz-Aguilar et al. 2008). Previous studies on gulls found severe impacts on breeding performance under different levels of food availability (Pons 1992, Pons and Migot 1995, Oro 1996). Particularly, our colony suffered a significant decrease in breeding performance (clutch size and egg volume) after landfill closure (Steigerwald et al. 2015). Moreover, Steigerwald et al. (2015) suggested that a dietary switch — which we confirmed — might not have been sufficient to fully cover the energy requirements of the local population. Foregoing reproduction to guarantee adult survival acts as a buffer mechanism against environmental variability and allows animals to cope with moderate environmental perturbations. Nevertheless, when food is in very short supply it can even affect body mass and local adult survival in long-lived seabirds (Oro and Furness 2002). This appears to be the case for our population, given the recorded drop in YLG body condition (Steigerwald et al. 2015) along with a slight decrease in local survival rates after landfill closure. Gulls usually form spatially structured populations (Oro et al. 2003) and given that previous studies have shown that dispersal occurs following environmental perturbations (Oro et al. 2004, Fernandez-Chacon et al. 2013), we suggest that food limitation has triggered not only mortality but also permanent emigration (through breeding dispersal) to neighboring populations (Bosch 2000, Oro 2003).

These findings agree with previous work on other seabird species (Oro 1999, Oro et al. 2004, Duhem et al. 2008), which found a close correlation between anthropogenic food availability and colony size. Our work suggests that the decrease in food availability caused a dietary shift towards marine resources. The dietary shift was followed by a partial reduction in breeding performance (Steigerwald et al. 2015), leading to an increase in mortality and dispersal. Finally, the cumulative effects of poisoning magnified an already severe decrease in population size through real adult mortality. Despite that many individuals might have died or emigrated from the study area, those remaining exhibited similar survival compared to pre-perturbation values. Another possible explanation for why population size and survival follow different response patterns after these perturbations is that poisoning was intended to cause non-selective mortality across the whole population, thus also affecting non-breeders and immature gulls, but our survival estimates came only from breeding adults. Alternatively, the termination of the waste food surplus might have decreased the carrying capacity of the system and the population size could therefore have declined to match this new population ceiling, while also influenced by the additive mortality from poisoning. We predict that population size will slowly increase in the coming years until it stabilizes at a new demographic equilibrium, however it will not reach the levels recorded before the two perturbations (Bosch et al. 2000).

1.5.1 Implications for the management of overabundant species

The food limitation and the mammal eradication campaign through poisoning were not specifically intended for the management of YLG populations. However, these actions allowed us to explore the implications of the combined effect in controlling of consecutive actions on the management of a so-called 'overabundant' species. Many populations of overabundant species of birds and mammals are subject to extensive management programs designed to control their numbers (Mate et al. 1998, Twigg and Kent Williams 1999, Anderson and Devlin 1999, Bosch et al. 2000). These actions mainly aim to either reduce breeding success (Thomas 1972, Merrill et al. 2006) or to eliminate adults by culling (Bosch et al. 2000, Baker and Harris 2006). Such management is expensive and ineffective in the long term if applied in isolation (Merrill et al. 2006, Baker and Harris 2006, Oro and Martínez-Abraín 2007). Here, we present evidence of how these two consecutively occurring perturbations have been extremely effective in reducing the population density of a generalist opportunistic bird, which has not recovered in the three years following these events. Under strong perturbation pulses (Martínez-Abraín et al. 2012) or intense environmental variability (Harding et al. 2011), the density dependent responses of demographic parameters appear insufficient to buffer population changes. Although an isolated perturbation, such as poisoning, seemed to have an important short-term effect, it is reasonable to believe that it was the closure of the landfill site that led to a permanent decrease in the carrying capacity of the system and hence a long-lasting reduction in population numbers, as previously suggested by Oro and Martínez-Abraín (2007). Cumulative effects of consecutive perturbations are likely to become a useful tool in the control of overabundant populations. Nevertheless, despite the potential that these results have for the implementation of more effective management actions of overabundant species, caution must be taken because their long-term consequences are still unknown.

1.6 Acknowledgements

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2

Consecutive cohort effects driven by density dependence and climate influence early life survival in a long lived bird

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2.1 Abstract

Conditions during early life, including maternal cohort effects, can influence the future fitness of individuals. This may be particularly true for long-distance migrating birds, because, apart from conditions experienced by cohorts during rearing, conditions during early-life in regions far from breeding grounds may also influence their population dynamics. Very little is known about the fitness consequences of those conditions experienced by juveniles after independence, especially in wild populations and for long-lived birds. We used multi-event capture-recapture-recovery models and a unique 26-year dataset for the Audouin's gull (*Ichthyaetus audouinii*) to assess for the first time whether survival was influenced by early conditions, both during the rearing period (i.e., a maternal cohort effect potentially affected by density-dependence) and the first winter (i.e., a cohort effect driven by climate when birds disperse to wintering grounds). Our results show that juvenile survival was highly sensitive to early-life conditions and that survival decreased with stronger density-dependence and harsh climate. The two consecutive cohort effects were of similar magnitude and they may represent a selection filter. Thus, early-life conditions had a strong impact on survival, and neglecting this complexity may hinder our understanding on how populations of long-lived animals fluctuate and respond to perturbations.

Key-words: Early-life conditions; survival; long-lived seabird; first year; density-dependence; winter.

2.2 Introduction

Conditions during early life can determine an individual's future fitness (Lindstrom 1999). Those conditions are known as cohort or silver-spoon effects and have been widely explored on a large range of vital rates in many taxa (see Appendix B.1, (Forchhammer et al. 2001, Reid et al. 2003, Le Galliard et al. 2010). Individuals facing harsh early-life conditions are expected to experience higher fitness costs later in life (Lindstrom 1999). Harsh conditions include unfavourable climate, high population size, low habitat quality, poor parental quality and low food availability, and their potential interaction (see Appendix B.1, (Forchhammer et al. 2001, Reid et al. 2003, Le Galliard et al. 2010, Hastings et al. 2011). The ability of offspring to compensate for a poor start in life determines whether early-life conditions have short- or long-term fitness consequences (Gaillard et al. 2003, Johan Solberg et al. 2004, Drummond et al. 2011) . The former, also known as numerical effects, involves changes in traits such as pre-breeding survival, birth weight, birth date and body growth; the latter, known as delayed quality effects, affects future breeding performance and thus results in changes in the age of first breeding attempts, lifetime reproductive success and adult survival (Christensen 1999, Metcalfe and Monaghan 2001, Forchhammer et al. 2001, Reid et al. 2003, Descamps et al. 2008, Marquis et al. 2008, Baron et al. 2010, Le Galliard et al. 2010, Hastings et al. 2011). Environmental forcing in early life drives complex trade-offs between vital rates and thus, many of the effects noted above are likely to be interrelated(Metcalfe and Monaghan 2001, Monaghan 2008). Overall, early-life conditions may generate differences in vital rates between cohorts and can have important demographic consequences. For instance, cohort differences may result in delays in a population's response to environmental conditions that could destabilize its population dynamics (Lindstrom 1999).

Comparatively, far more attention has been directed at explaining the effects of early-life conditions on reproduction rather than on survival (Metcalfe and Monaghan 2001, Watson et al. 2015). Within survival studies, substantial research describes the effects of early-life conditions under controlled experimental conditions (Van de Pol et al. 2006, Hastings et al. 2011) but much less is known about wild populations of long-lived species (Van de Pol et al. 2006, Baron et al. 2010, Hastings et al. 2011). Additionally, it is likely that the processes underlying the strong early-life selection pressures on survival, which lead to high and stable adult survival rates in long-lived species, are not limited to the rearing period (Sergio et al. 2011). For example, conditions experienced during winter may give rise to important changes in demographic rates such as recruitment, dispersal and even survival (Sanz-Aguilar et al. 2012). Nevertheless, winter conditions have been seldom considered as a type of cohort effect, even though these conditions may primarily affect juveniles. Thus, first-winter conditions are likely to play a key role in the dynamics of natural populations, and their integration into early-life condition studies should therefore be considered. Yet, in some long-lived species and particularly in birds, juvenile stages are often elusive and information about critical periods other than the breeding period is scarce (Fay et al. 2015).

Here, we explore the potential survival costs of a bad start in life in a long-lived bird, the Audouin's gull (*Ichthyaetus audouinii*). We tested the survival costs associated with the conditions experienced by individuals during two critical early-life periods: the rearing phase and their first winter. Food is a key factor shaping population dynamics. Density-dependence and climate, which regulate food availability, are likely to be crucial during these two life phases (Oro et al. 2004). We predicted that individuals belonging to cohorts experiencing harsh environmental conditions during its first year (i.e., low food availability during both rearing and wintering periods) would endure greater survival costs later in life. In addition, we predicted that, since the study species is a long-lived bird, these effects would be strong in the first years of life and weak or non-existent on adult survival (Drummond and Ancona 2015, Fay et al. 2015).

2.3 Material and methods

2.3.1 Demographic data

We collected demographic data in Punta de la Banya (Ebro Delta, Spain; 40°37′ N, 00°35′ E), a flat sandy peninsula of ca. 2600 ha. The site holds ca. 60% of Audouin's gull's world population (Fernandez-Chacon et al. 2013). During 1988–2012 a total of 24038 chicks were individually marked at fledging using a plastic band with a unique alphanumeric code. A total of 33322 resightings and 552 recoveries were used in the analyses. Resightings were made during the breeding season (April–July) using spotting scopes. Recoveries of dead birds took place at the study site (authors' own fieldwork) and abroad (information provided by ringing offices).

2.3.2 Environmental data

We tested whether survival was affected by conditions experienced during the rearing period and after independence, during the first winter along the NW African coast. As a proxy of rearing conditions we used food availability per capita (Almaráz and Oro 2011, Oro et al. 2013b). Audouin's gull is a long-lived seabird that breeds colonially from April to July and usually lays three eggs. The species feeds mainly on small pelagics (Oro et al. 1997), and discards from trawling fleets can represent up to 75% of their diet during the breeding season (Oro and Ruiz 1997). In the study area, La Ràpita is the most important fishing harbour and accounts for 60% of the catch in number and 74% in total power. Thus, we took trawling landings at La Ràpita as a proxy of food availability in June, when chicks are under parental care. We then divided this proxy of food availability by population size of both Audouin's and Yellow-legged gulls (Larus michahellis), the most abundant sympatric species that exploits discards (Oro and Ruiz 1997), to account for density dependence of the guild through interference competition and obtained the proxy of food availability per capita (hereafter DD). As a proxy of first winter conditions, we used the North Atlantic Oscillation climatic index during December–March (hereafter W_{NAO}), because gulls disperse during winter mostly to the Senegambia region (Oro and Martinez 1994). This long-distance dispersal decreases with age, and most birds do not cross to Africa as they become older (Fig. 6)(Oro and Martinez 1994).

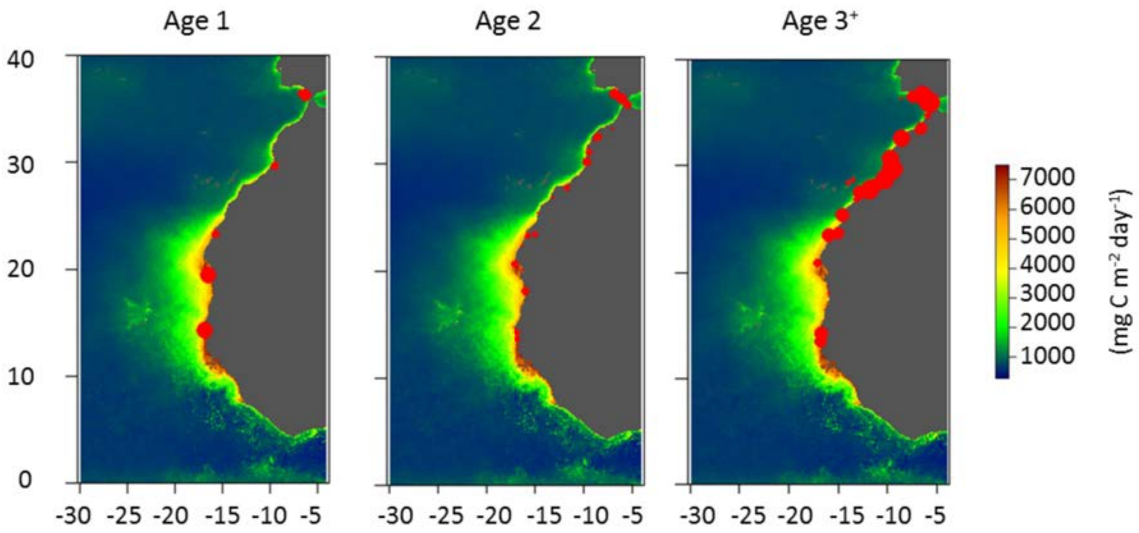

Fig. 6: First winter conditions for Audouin's gulls, expressed as the average winter net primary production during 2002–2012 ($mgCm^{-2}day^{-1}$) on the Northwest African coast, which influenced the availability of small pelagics. Left panel represents first winter resightings of animals marked at the Ebro Delta (red dots), whereas right panels show those resightings for older birds (red dots). The size of red dots is proportional to the number of individuals resighted. Resighting data were provided by the Catalan Ringing Office (`<www.ornitologia.org>`).

High positive W_{NAO} values are associated with the intensification of upwelling and thus with higher small pelagic fish availability (Hurrell et al. 2003). DD and W_{NAO} index are independent of each other ($R^2 = 0.011$, $p = 0.636$).

2.3.3 Modelling and hypothesis testing

Models were constructed in a multi-event capture-recapture framework, which addresses state uncertainty by relating the true state of the individual to the observed event via a series of conditional probabilities (Pradel 2005). Goodness of fit test (GOF, see Appendix B.2) suggested the presence of both trap-dependence and transience effects. After accounting for them, an acceptable variance inflation factor of 1.42 was obtained and used to correct all models constructed in E-SURGE (Pradel et al. 2003, Choquet and Nogue 2010). Based on the GOF results we built models with four states (Aa, alive and trap-aware; Au, alive trap-unaware; Dr, recently dead and Dl, dead long ago) and three events (0, not seen; 1, seen alive and 2, seen dead) (see Appendix B.3). We used previous knowledge of the species (Oro et al. 1999, Oro and Pradel 2000, Genovart et al. 2012) to design our initial exploratory set of models and select the best general model structure based on QAICc criterion (see Appendix B.4)(Burnham and Anderson 2002). We tested the absence of long-term cohort effects by running additive and interaction models including cohort and age effects.

Once confirmed, we used the best general model to run different models including the effect of DD and W_{NAO} in early-life and their additive and interaction effects. Finally, we calculated the fraction of temporal variation explained by each covariate (DD and W_{NAO}) using ANODEV (Grosbois et al. 2008)(see Appendix B.5, Table 13). This was first tested in the general model with the best age structure and then in each of the young age-classes in order to evaluate their temporal extent.

2.4 Results

The best recapture structure retained three age classes with different recapture probabilities, time and a trap awareness effect ($STEP1$, see Appendix B.4). The model including temporal variation in recovery probabilities performed the best ($STEP2$, see Appendix B.4, Table 12) and the best structure for survival included five age classes with an interaction with year ($STEP3$, see Appendix B.4, Tables 12 and B.6, Table 14 for model estimates, Fig. 7). We also evaluated the potential effects of early-life environmental covariates on survival. Models including DD and W_{NAO} covariates performed poorly in terms of QAICc compared to the best model, the time varying model (see Appendix B.7, Table ??), but they explained large proportions of survival variability. DD explained 34% of survival variability, W_{NAO} explained 17% of survival variability, and the models including additive and interaction effects explained 42% and 50% of survival variability respectively (see Appendix B.8, Table 16, all $p \leq 0.002$).

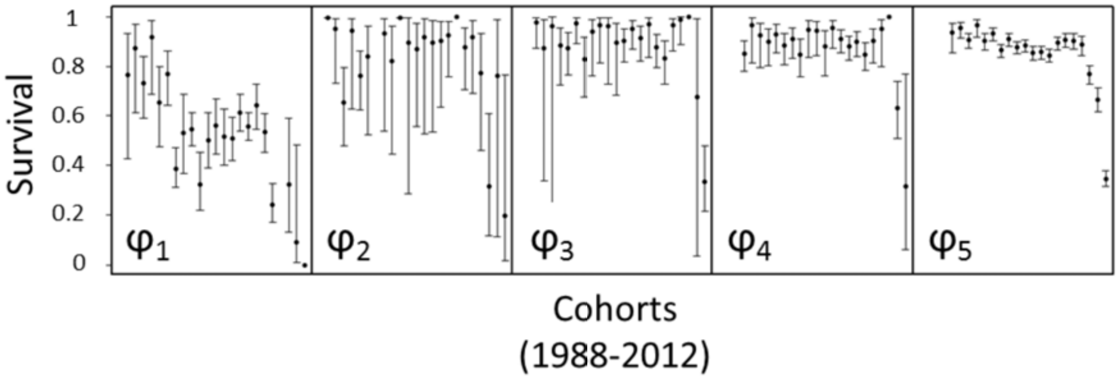

Fig. 7: Annual survival (95% CI) of Audouin's Gulls breeding in the Ebro Delta in 1988–2012 (each panel represents one of the five age classes retained by the best model; see Appendix B.7,??).

Once the effect of both DD and W_{NAO} had been confirmed, we evaluated their effects on each of the five ages considered. DD and W_{NAO} had a strong influence on Audouin's gull survival but the effect faded after the first year of life (beta estimates, β and 95% confidence intervals CI) for first-year survival $\phi 1$: $\beta_{DD} = 0.625\ (0.248, 1.001)$, $\beta W_{NAO} = 0.464\ (0.376, 0.551)$ see Appendix B.8, Table 16 showing β estimates for each model). Offspring born under high food availability per capita and those that experienced mild first winters (high W_{NAO} values) had increased first-year survival rates. DD and W_{NAO} explained similar amounts of survival variability — about 50% of first-year survival ($p = 0.000$; see Fig.8 and Appendix B.9, Table B.9). The model including both DD and W_{NAO} conditions explained a significant 62% of first-year survival ($F_{2,19} = 15.52$, $p < 0.001$, see Appendix B.9, Table B.9). Models including an interaction effect do not explain any extra variance compared to the models including only the additive effect.

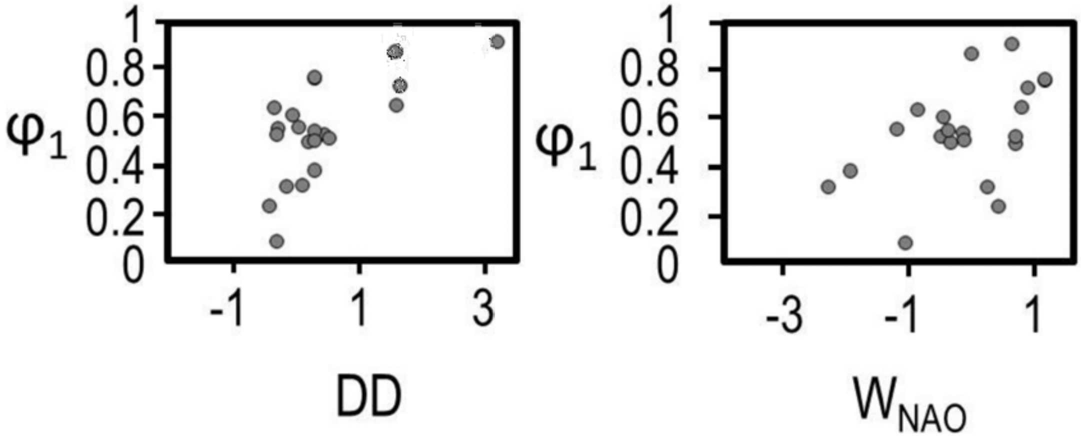

Fig. 8: Relationship between first year survival ($\phi 1$) of Audouin's gulls breeding in the Ebro Delta and tonnes of fish landed by trawlers per capita, including Audouin's and yellow-legged gulls (DD); and Northern Atlantic Oscillation index (W_{NAO}) during the first winter of life.

2.5 Discussion

Several previous studies show that the effects of early-life conditions on fitness components can be important: the harsher the conditions an individual experiences during early life, the higher fitness costs the individual will undergo (Lindstrom 1999, Gaillard et al. 2003, Le Galliard et al. 2010, Hastings et al. 2011). However, few studies have attempted to unravel the fitness consequences of early-life conditions in critical periods other than the rearing period, especially in wild populations (Hastings et al. 2011). We evaluate for the first time both the effects of early-life conditions experienced during rearing, but also during the first winter on the survival of a long-lived bird. Here, we find that both rearing and first winter conditions influenced first year survival. Although harsh early-life conditions can have consequences for long-term fitness, their influence is usually most pronounced during early life stages (Lindstrom 1999, Metcalfe and Monaghan 2001). We also show here that in Audouin's gulls, harsh early-life conditions strongly influenced first-year survival but that influence fades at older ages. The mechanisms driving trade-offs of poor early-life conditions in future fitness are likely to respond to complex causal routes and they remain fairly unknown. Thus, we cannot ascertain whether what we observed was the result of compensatory effects, acquired resilience, life history trait plasticity or a combination of those processes (Metcalfe and Monaghan 2001, Drummond and Ancona 2015). Previous studies suggest that early-life conditions might act as selection filters by eliminating frail individuals from the population, and leading to stabilization of adult survival at high values by environmental canalization typical for long-lived species (Stearns 1992, Gaillard et al. 1998, Monaghan 2008, Kendall et al. 2011). Our results suggest that a strong selection filter operate on this species at least during the first year of life, eliminating those frail individuals, and the strength of mortality during this period depends on the severity of environmental conditions during early life. Therefore, rearing and first winter periods seem to be operating as two consecutive cohort effects likely resulting in a positive selection for high-quality phenotypes (Sergio et al. 2011). In our study, food competition by density-dependence was a key factor driving the effects of early-life conditions on survival. Breeding gulls intensively exploit trawler fleet discards, and food availability per capita during the rearing period is positively related to improved chick body condition and higher reproductive success (Oro et al. 1996, Oro and Ruiz 1997). We show here that food availability per capita for breeders during rearing also improves future survival of newborns. This cohort effect during the rearing period can be considered a maternal effect because the environment experienced by the mothers influences the future performance of their offspring. After fledging, juveniles disperse and winter in the Senegambia region, where they mainly feed on small pelagic fish shoals (Oro and Martinez 1994). Climatic conditions during first winter also influenced juvenile survival. Positive W_{NAO} is associated with the strengthening of the African Coast upwelling and increasing the availability of small pelagics (Pedlosky 1978, Barber and Chavez 1983, Santos et al. 2005). Therefore, higher food availability during first winter period improves juvenile survival. Our results agree with our expectations on the survival components of fitness; that is, individuals suffering from food limitation during their early life, both during rearing and first winter, suffer fitness costs (Breton and Diamond 2014).

We found that individuals born in years when there was lower competition for foraging resources survived better in their first year of life. When individuals attempt to exploit a common limited resource, competition occurs (Begon et al. 1996). The degree of competition depends on both the absolute resource availability and the number of individuals exploiting that resource. Hence, this is a density-dependent process (Begon et al. 1996, Krebs 2001). Competition is common in natural populations and so its effect is implicitly accounted for in most early-life condition studies (Van de Pol et al. 2006, Breton and Diamond 2014). Such studies include either population size or resource availability as competition proxies and many have found strong density-dependent effects for different fitness components (King 2002, Durant et al. 2003, Grande et al. 2009). However, we suggest that, when available, the combination ‘resource availability per capita’ is likely to be a more accurate proxy for density-dependence driven by competition. Density-dependent effects on juvenile survival have been widely reported, especially in mammals and birds (Forchhammer et al. 2001, Van de Pol et al. 2006, Bonenfant et al. 2009, Hastings et al. 2011). These studies suggest that this demographic trait and, particularly, first-year survival are the most affected by density-dependence. However, these survival rates are also likely to be the most variable over the years since they have not been environmentally canalized. Environmentally induced responses are often complex and lead to covariance processes within demographic traits (Coulson et al. 2005, Herfindal et al. 2014). For instance, a decrease in density-dependence during rearing increased not only survival rates of gulls (our study), but also the reproductive performance of breeders (Oro et al. 2013b). These variations in how individuals from different cohorts respond to environmental conditions act as a structuring force in population dynamics, because cohorts of individuals might differ considerably in their future performance (Beckerman et al. 2002, Benton et al. 2006). The influence of age and environmental variability over the years on several life-history traits and population dynamics has been extensively studied in many taxa, but the potential influence of cohort effects has been seldom considered (Coulson et al. 2001a). For instance, a cohort of individuals reaching sexual maturity synchronously and beginning to breed in a harsh reproductive season can pay a reproductive cost with reduced survival and lifetime reproductive success. Furthermore, the next cohort of offspring could inherit the effects of this bad maternal environment. Thus, we highlight here the relevance of monitoring early-life phases for understanding their sensitivity to environmental conditions and the potential consequences for population dynamics. Although life-history theory predicts that adult survival will be the key parameter driving population functioning, juvenile survival has recently been acknowledged as an important source of variability in population dynamics (Gaillard et al. 1998, Grande et al. 2009, Sergio et al. 2011). Here, we present the first evidence on how both rearing and first winter conditions shape the survival of the first year of life via density-dependence and climate effects. These two consecutive cohort effects synchronously influence the survival of individuals born in the same season and suggest the existence of delayed life-history effects, such as variability and delay in density-dependence in population dynamics (Beckerman et al. 2002). The incorporation of these findings into fitness studies and future population models will provide a better understanding of complex population dynamics.

3

Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers

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3.1 Abstract

Studying colonisation is crucial to understand metapopulations, evolutionary ecology and species resilience to global change. Unfortunately, few empirical data are available because field monitoring that includes empty patches at large spatiotemporal scales is required. We examine the colonisation dynamics of a long-lived seabird over 34 years in the western Mediterranean by comparing population and individual data from both source colony and the newly-formed colonies. Since social information is not available, we hypothesize that colonisation should follow particular dispersal dynamics and personal information must be crucial in decision making. We test if adverse breeding conditions trigger colonisation events, if personal information plays a role in colonisation and if colonisers experience greater fitness. Our results show a temporal mismatch between colonisation events and both density-dependence and perturbations at the source colony, probably because colonisers needed a longer prospecting period to compensate for the lack of public information. Colonisers were mostly experienced individuals gaining higher breeding success in the new colony. Our results highlight the demographic value that experienced individuals can have on metapopulation dynamics of social long-lived organisms. .

Key-words:Colonisation, dispersal, information, patch, threshold.

3.2 Introduction

Species persistence in a changing world depends on the ability to respond to environmental changes (Slatkin 1987, Gilpin 2012). A mechanism by which species can cope with such changes is by modifying their spatio-temporal distribution and colonising new environments (Gilpin 2012). Unfortunately, the empirical study of colonisation has been largely anecdotal — mostly in non-social species and through theoretical models Pokki (1981), Doak (2000) . Colonisations occur at large spatio-temporal scales and are seldom documented, particularly in long-lived vertebrates (Storey and Lien 1985, Oro and Ruxton 2001). Therefore, more information on colonisation processes (e.g., drivers and fitness consequences) and the individual characteristics of colonisers (e.g., experience or age) (Coulson and Neve 1992, Oro and Ruxton 2001) is required.

Dispersal is a multi-step decision process: Individuals must first decide to disperse from their natal or breeding colony; then, individuals must decide between settling in an already occupied site or colonising a new empty patch (Kharitonov and Siegel-Causey 1988, Fernandez-Chacon et al. 2013). These decisions require reliable information — anything reducing uncertainty — about the alternatives (Danchin et al. 2004). Such decisions are more likely to lead to positive outcomes if based on information, reducing uncertainty about the suitability of alternatives(Danchin et al. 2004). Colonisation is thus a risky endeavour since social information may not be available (or only available through heterospecific habitat copying) and individuals must rely solely on personal information.

Until the 2000's the Audouin's gull (*Ichthyaetus audouinii*) colony at Punta de la Banya (hereafter, source colony) was the most important breeding site hosting up to 70% of the species' world population (Fernandez-Chacon et al. 2013). During the last three decades, around 20 new Audouin's gull colonies formed along the western Mediterranean providing us with a unique dataset to study patch colonisation. We address three specific questions (1) Do adverse breeding conditions trigger colonisation? (2) Does personal information play an important role? (3) Do colonisers experience greater fitness? We hypothesize that personal information is relevant. We expect to find: (a) a temporal delay between perturbations triggering dispersal and colonisation (i.e., an amount of time required to explore empty patches and to gather information), (b) that colonisers should be experienced breeders (i.e., previous breeding experience might reduce uncertainty), and (c), since choosing a breeding patch is a risky decision, colonisation should lead to increased population fitness (i.e., higher breeding success) (Forbes and Kaiser 1994).

We searched for qualitative association with adverse breeding conditions by identifying breaking points on the temporal distribution of colonisations. Then, we tested the role of experience in one of three different ways: Firstly, we tested for differences in the proportions of inexperienced and experienced breeders present at new colonies and the source colony. Secondly, we compared the proportion of successful and unsuccessful breeders (BS_{qt-1}) that decided to return and breed again at the source colony or to settle in a new colony. Thirdly, we tested for differences in the laying date (LD), clutch size (CS) and egg volume (V) at the source colony in the year preceding colonisation (t-1) between newly colonizing individuals and philopatric birds (t). Finally, we compared breeding success of a new colony (La Ràpita Port) with the source colony, and specifically with two sub-colonies (i.e., patches) within the source colony with similar age distribution but differing in habitat features related to accessibility for predators.

3.3 Material and methods

Audouin's gull is an endemic Mediterranean seabird (Oro et al. 2011). Until the mid-2000s, 70% of their world population was concentrated in the Punta de la Banya (source colony, Ebro Delta, $40°37'N$, $00°35'E$) (Fernandez-Chacon et al. 2013). However, from 2002 a series of new colonies became established in the western Mediterranean (Fig. 9, Table 7 and Appendix C.1).

Table 7: Names of new colonies formed during the study (see Fig.9 for location), and their characteristics: type of habitat; year of colonization and number of pairs in the establishment year. New colonies are sorted by year of colonization, except for Columbretes Is, which was likely settled before. Punta de la Banya is the source colony (Fernandez-Chacon et al. 2013). * Colonies used to assess age structure.

Site	Habitat	Year	Pairs
Columbretes	Rocky island	1974	45
Punta de la Banya*	Brackish marshes and salt-pans	1981	23
Grosa	Rocky island	1993	300
Albufera	Shallow coastal lagoon	2003	6
El Saler	Artificial coastal lagoon	2004	1
Torrevieja	Salt-pans	2005	30
Benidorm	Rocky island	2006	3
Tomás Maestre	Port	2006	11
San Pedro	Salt-pans	2006	18
Almenara	Shallow coastal lagoon	2009	5
Llobregat*	Artificial riverine island	2010	140
Escombreras	Port	2010	3
Buda	Brackish marshes	2011	1
Castellón*	Port	2011	303
La Ràpita*	Port	2011	2609
Sollana	Shallow coastal lagoon	2012	1
Tarragona*	Port	2013	19
Barcelona*	Port	2013	69
Sant Antoni*	Brackish marshes and salt-pans	2014	116
Valencia	Port	2014	239

A long-term monitoring and mark-capture-recapture program was established at the source Ebro Delta colony and has been running since 1981, which allowed us to evaluate possible drivers of colonisations (Payo-Payo et al. 2016).

3.3.1 Environmental and breeding performance variables

We used several environmental factors as proxies of adverse breeding conditions: density of aerial nest predators and intra-guild competitors such as the yellow-legged gull Larus michahellis (N_{Lm}/N_{La}, yellow-legged gull population size divided by Audouin's gull population size to account for density-dependence,Oro et al. (2006)); presence of a single badger (*Meles meles*) that predated on nests in 1994; regular presence of foxes (*Vulpes*

vulpes) preying on nests and adults from 1997 onwards; and extreme weather conditions in 2008 (namely, a strong cold storm that killed most chicks) (Oro 1999, Martínez-Abraín et al. 2003, Oro et al. 2008, Almaráz and Oro 2011).

Moreover, we also used Audouin's gull breeding success as a proxy of adverse breeding conditions. Breeding success was first calculated qualitatively (BS_q), categorizing marked individuals as unsuccessful (0, no hatchlings) or successful breeders (1, at least one hatchling); then quantitatively at a population level (BS_p) by dividing the number of chicks by colony size (number of pairs). Number of chicks was estimated by capture-mark-recapture using the Lincoln-Petersen estimator and colony size by counting nests using linear transects (Williams et al. 2001, Oro et al. 2011, Seber 2002). Breeding success data were available for the source colony and for only one of the newly established colonies (La Ràpita Port).

We considered individual age as a proxy of breeding experience. Most Audouin's gulls in the source colony recruit at the age of 3 and 4. Therefore, we categorized individuals as inexperienced (3-4 years old) vs. experienced ($\geq$ 5 years old) (Oro and Pradel 2000). Age of individuals was available for 6 colonies in the year of colonization (Llobregat, Castellón port, La Rapita port, Tarragona port, St. Antoni and Barcelona port) and for the source colony (Punta de la Banya) (Fig.9 and Table 7). Since the number of individuals colonising each site was commonly low, we lumped resighting data from all 6 new colonies together and compared their age structure with the age structure at the source colony the same years these new colonies were established (2010, 2011, 2013 and 2014, Fig.9, Table 7).

Finally, as proxies of breeding performance we recorded the breeding phenology (LD, laying date of the first egg as the number of days elapsed since 1st of April, n=31), clutch size (CS, the number of eggs laid by clutch, n=50) and egg volume (V, n= 50). Egg volume (in cm^3) was calculated using the equation: $V = \beta LW^2$, in which β was a species-specific constant parameter ($\beta = 0.476$ for Audouin's gull (Harris 1964, Oro et al. 1995), L was egg length and W was egg width, the two expressed in cm. All measures were completed with a digital calliper to the nearest millimetre.

3.3.2 Data analyses

We first assessed the existence of an association between adverse breeding conditions and colonization events. To do this, we calculated the natural logarithm of the accumulated frequency of new colonies over time and searched for breaking points using Bayesian analysis of change point problems implemented in the 'bcp' R package (Erdam and Emerson 2007). Breaking point analyses detects points that divide data series into blocks such that the mean is constant within each block using the Bayesian statistic framework (Wang and Emerson 2015). We then qualitatively assessed if there was a temporal association between the resulting breaking points and different adverse breeding conditions (badger and fox presence and extreme weather events), density dependence (N_{Lm}/N_{La}) and breeding success (BS). We assessed if there were differences in the proportions of inexperienced and experienced breeders present between the new and the source colony (n=827 and 4810 individuals, respectively) by means of a contingency table and a test. We tested the hypothesis that individuals having poorer breeding performance the year before were more likely to colonize a new patch than those experiencing high breeding performance in three different ways. First, we used count data, a contingency table and a test to compare the proportion of successful and unsuccessful breeders (BS_{qt-1}) that, having bred at the source colony in the year previous to the colonization (n=124), decided to return and breed again at the source colony (n=102) or to settle in a new colony (n=22). Second, we used individual data and binomial logistic regression (0=source colony, 1=new colony) to test the effect of previous breeding status (successful and unsuccessful) as an explanatory variable for colonization. Third we tested differences in laying date (LD), clutch size (CS) and egg volume (V) in the year previous to the colonization (t-1) in the source colony by individuals present at new (n=91) and source colonies (n=109) the year of colonization (t). To test for differences in LD_{t-1} and CS_{t-1} we used linear models, and to test for differences in V_{t-1} we used general linear models including nest identity as a random factor (For details see Steigerwald et al. (2015)).

We tested the hypothesis that individuals breeding at new colonies should experience higher breeding success by comparing breeding success at the new colony with breeding success at the source colony the year of colonization. At the source colony, breeding individuals are spatially aggregated in discrete dunes and dikes (i.e., patches) — each of these spatial aggregations is considered a sub-colony which usually has a different age distribution of breeding individuals (Genovart et al. 2003) and habitat characteristics. To eliminate any confounding effect of a different age distribution, we first tested for differences in breeding success with the whole source colony, and then with two sub-colonies (Sub1 called Miseria and Sub2 called Alfacs) within the source colony. These sub-colonies had similar age distributions to the new colony (La Ràpita Port) and differed from one another in their accessibility to terrestrial predators.

Models were selected using the Akaike Information Criterion corrected for overdispersion (AIC_c, Burnham and Anderson (2002)). We considered the model with lowest AICc as the best model, and those within two ΔAIC_c (the difference in AIC_c values) to be statistically equivalent (Burnham and Anderson 2002). All analyses were implemented using the R software.

3.4 Results

Since 1981, and particularly since 2003, 19 new colonies were established along the western Mediterranean (Table 7, Fig.9-10, see a video of colonisation process in Supplementary material Appendix C.1). We detected high probabilities of breaking points — points that divide data series into blocks such that the mean is constant within each block — in 1992, 2003, 2005 and 2010 (Fig.10.c). This analysis identified three major phases: (a) a 1992 breaking point corresponded with the formation of Grosa colony, (b) colonisation events in 2003 and 2005 coincided with colonisations of six mostly natural sites in the southern part of the study area, and (c) the colonisation of port sites in 2010 (Fig. 9). 37% of the new colonies appeared inside or near ports (Fig. 9). There was no obvious linkage of colonisation events to adverse breeding conditions in the previous breeding seasons (Fig. 10).

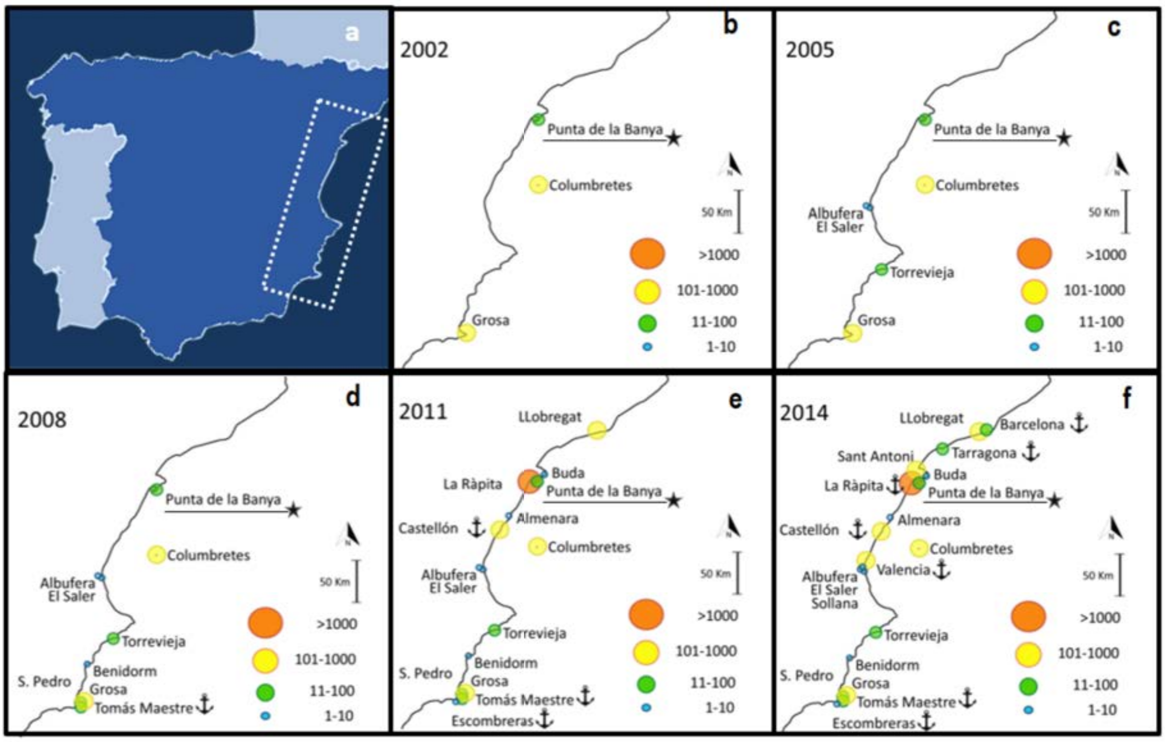

Fig. 9: Panel a) Iberian Peninsula and study area along the western Mediterranean coast (surrounded by white dashed line). We did not include colonies from the Balearic Islands since they have little exchange of individuals with the mainland system (Fernandez-Chacon et al. 2013). Panels b) to f) show the temporal evolution of Audouin's gull colonisation events at regular time intervals from 1975. Circle size is proportional to the number of colonisers in the year of colony foundation; anchors indicate colonies settled in port areas (see Table 1 for colony details). Video with complete temporal evolution in Appendix C.1. Punta de la Banya is the source colony (underlined and marked with a star, Fernandez-Chacon et al. (2013)). Maps were built in R-Software (Team 2013).

In the first year of colonisation, new colonies hosted higher proportions of experienced individuals than the source colony (87.1% and 63.5%, respectively, $\chi^2 = 176.895$, df=1, $p < 0.0001$). There was no difference in the proportion of previously successful breeders between the new and the source colony in the year of colonisation (BS_{qt-1}, $\chi^2 = 0.739$, df=1, p = 0.390). In other words, settlement colony (source vs. new) was not related to the breeding success experienced by individuals the previous year (see Appendix C.2, Table 18). Colonisers and philopatric individuals also showed similar egg volume, clutch size and laying date in the year before colonisation (see AppendixC.2, Table 19).

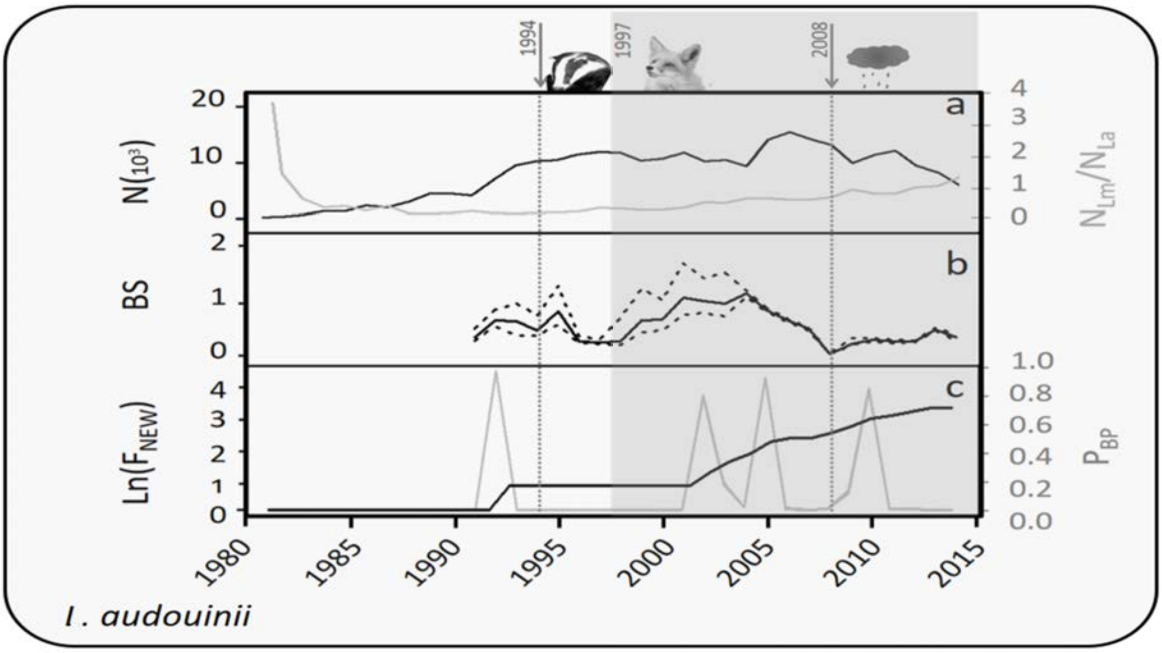

Fig. 10: Arrows show punctual presence of a badger and an extreme cold storm in different years; shadowed area denotes continuous presence of foxes; Panel a) Audouin's gull population density fluctuations (black solid line, number of pairs $N * 10^3$); N_{Lm}/N_{La}, ratio of population size between Yellow-legged and Audouin's gulls (grey solid line). Panel b) BS, Audouin's gull breeding success at the Ebro Delta colony (number of chicks/pair, ($95\%CI$)). Panel c) Ln (F_{NEW}), neperian logarithm of the accumulated frequency of new colonies by year in the Western Mediterranean (black solid line) and PBP, probability of breaking points for the Ln (F_{NEW}) temporal series (grey solid line). Fox and Badger images were modified from the Flirck photos 'redfox10' and 'Badger' which are copyright (c) 2011 Peggy cardigan `<https://flic.kr/p/kFvEbZ>` and (c) 2012 Peter Trimming `<https://flic.kr/p/d5CkEJ>` respectively. Both images can be used under a CC by 2.0 `<https://creativecommons.org/licenses/by/2.0/>`.

In the year of its colonisation (2011), breeding success (BS_{pt}) was higher at the new colony (La Ràpita Port), BS_{pt}= 0.31(95% CI, 0.29-0.34), than at the source colony, BS_{pt}= 0.14 (95% CI, 0.13-0.15), and at both source sub-colonies with a similar age structure to the new colony, BS_{ptsub1} = 0.24 (95% CI, 0.18-0.29) vs BS_{ptsub2} = 0.1(95% CI, 0.07-0.12) (Fig.11). In 2011, the new colony was free of predation, as was one sub-colony at the source which was surrounded by water (Sub1), preventing access by terrestrial predators. The other sub-colony (Sub2), as with many sites at the source colony, suffered from intense carnivore disturbance and predation. Colonies that were more accessible to terrestrial predators experienced lower breeding success (Fig.11).

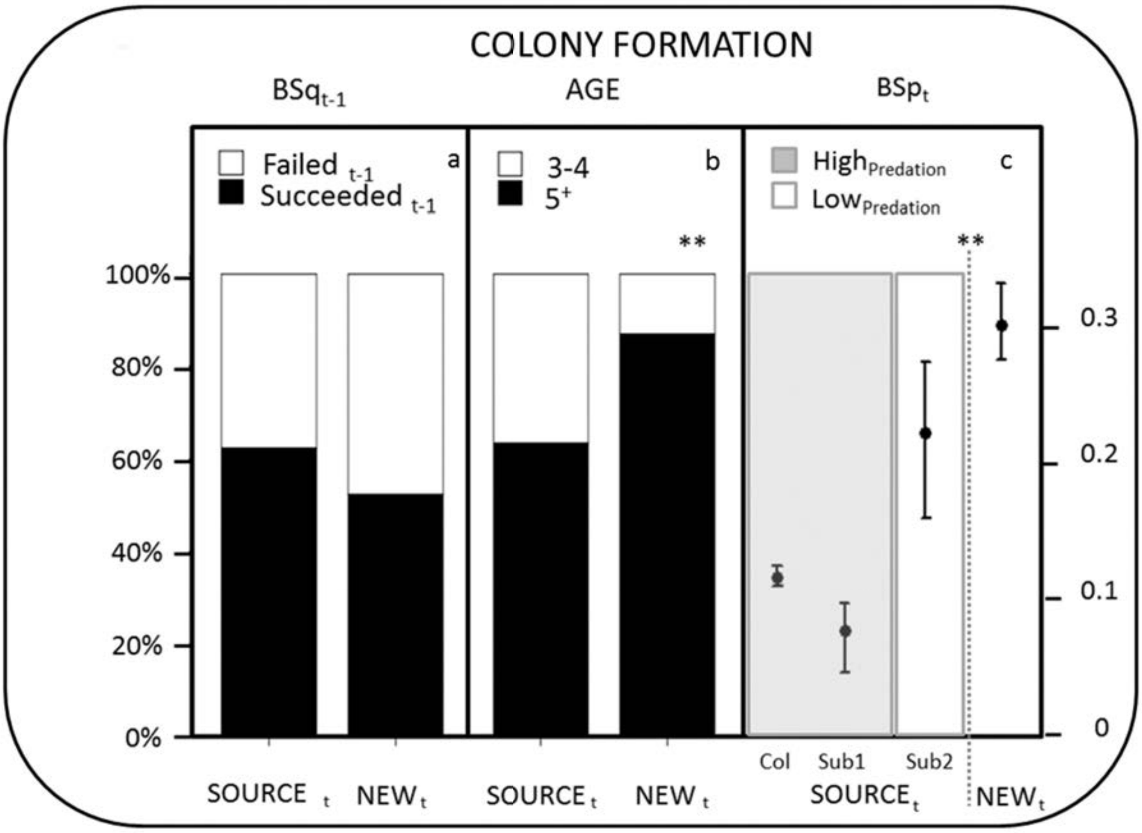

Fig. 11: SOURCE refers to individuals present at the Punta de la Banya colony and NEW to individuals present at new formation colonies. Panel a) represents proportion of individuals present in SOURCE colony and NEW colonies at time t, conditional to their breeding success at t-1 (failed vs succeeded). Panel b) represents distribution of individuals by means of breeding experience: inexperienced 3-4 years (white) vs experienced 5 years or more (black). Panel c) represents breeding success of SOURCE colony and NEW colonies at time t with high (grey shadow) and low (no shadow) predation levels. Notice that SOURCE colony includes the average breeding success of individuals breeding at different sub-colonies (patches) at the source colony (Col), and Sub1 and Sub2 are the two sub-colonies within the SOURCE colony with similar age structure to the NEW colony (see Methods) (Sub1, Miseria and Sub2, Alfacs. $^{**}p < 0.001$ significance level).

3.5 Discussion

Colonisation is a crucial process in metapopulation dynamics and may be critical when assessing a species' ability to respond to perturbations (Slatkin 1987, Gilpin 2012). Its drivers, the characteristics of colonisers and a quantification of its pay-offs remain fairly unexplored (Storey and Lien 1985, Forbes and Kaiser 1994, Oro and Ruxton 2001). Our results show that colonisations seem temporally and spatially unpredictable and they occur in response to an accumulation of perturbations exceeding an unknown threshold. Compared to source colonies, a disproportionate number of colonising individuals were older birds with greater breeding experience. In turn these birds had higher breeding success at newly established breeding colonies. The temporal mismatch between adverse breeding conditions and colonisations may be in response to several processes which might not be mutually exclusive. First, individuals may face a trade-off between being philopatric, thus taking advantage of their previous experience and colonising a new patch without experience or social information available (Danchin et al. 2004). At the source colony, higher occupation of sites surrounded by water was likely a behavioural resilience mechanism to mitigate the effects of predation and to avoid the inherent risks of colonisation (Oro et al. 2009). This behavioural resilience may delay colonisations of new patches, but it probably has a threshold, particularly when perturbations are consecutive (Almaráz and Oro 2011, Payo-Payo et al. 2015). Second, several studies have recorded some individuals visiting empty patches years before breeding, probably to collect information about habitat suitability (Anderson 1982, Danchin et al. 2004, Arroyo Morcillo and Fernandez 2015, Martinez-Vilalta and Motis 1982). Resilience and philopatry may thus delay the appearance of tipping points in colonisation, and may result in a non-linear relationship between adverse breeding conditions and colonisation (Solé and Bascompte 2006). The use of non-natural environments (i.e., ports) appeared as a cultural innovation for the species in the study area, in a similar manner to that which occurred in a naval port in Corsica in 1990 (Recorbert 2010). This innovation suggests adaptation to novel environments, and the spread of port colonisations in recent years suggests that colonisers rely on experience and obtain information from already occupied patches to reduce uncertainty (Danchin et al. 2004).

Previous studies at the source colony showed that predation caused partial breeding failure and immediate high dispersal to already occupied patches (Almaráz and Oro 2011). Nevertheless, colonisations did not occur immediately after deterioration of breeding conditions. Colonisation seems to follow special dispersal dynamics. Colonisers were experienced individuals that may be followed by young and inexperienced individuals in subsequent years, once the patch is occupied (Anderson 1982, Storey and Lien 1985, Tims et al. 2004, Fernandez-Chacon et al. 2013). Colonisation should only occur when advantages of colonisation outweigh its risks (Forbes and Kaiser 1994). We detected higher breeding performance at the new colony probably due to lower predation risks. Increased fitness should be expected following successful colonisations (i.e., colonies persisting over time); however, that might not always be the case since, given the lack of public information at non-occupied patches, the ability to interpret their suitability is necessarily imperfect (Forbes and Kaiser 1994, Almaráz and Oro 2011). Nearly 50% of the new colonies disappeared a few years (or even a single year) after colonisation (Oro et al. 2003). Little evidence was available regarding breeding performance during the first years after colonisation events and it did not show a clear pattern (Storey and Lien 1985, Tims et al. 2004, Kildaw et al. 2005). In summary, we show that breeding experience and longer prospecting periods might be necessary for colonisation. Until now, dispersal theory failed to acknowledge the role of personal information in colonisation for social species (Pokki 1981, Doak 2000, Fernandez-Chacon et al. 2013). Future attempts to understand colonisation in social species should focus on how individuals manage and reduce uncertainty when assessing patch suitability (Forbes and Kaiser 1994). Population models should account for the higher demographic value of experienced breeders since metapopulation dynamics might be more sensitive to those individuals than previously thought. Our results have significant implications for metapopulation ecology but especially for the understanding of how social species respond to environmental change (Slatkin 1987, Gilpin 2012).

4

Population changes in age structure and reproductive value driven by non-lethal perturbations of mesopredators

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Content of this chapter has been submitted to: Proceedings of the Royal Society of Biology B

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Data is deposited in the CEDAI Repository:
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4.1 Abstract

Intensification of perturbation regimes due to global change should increase environmental variability experienced by individuals, promoting substantial changes in population dynamics. For instance, perturbations can affect population dynamics through lethal effects by significantly increasing mortality. However, the role of non-lethal effects causing disturbance such as physiological stress (potentially affecting breeding performance) and behavioural responses, has been comparatively overlooked and their potential population effects remain obscure. During the last 23 years we developed a mark-recapture program for the Audouin's gull (*Ichthyaetus audouinii*) and an intensive carnivore monitoring to assess how dispersal as a non-lethal effect of the appearance of predators in a previously predator-free area may affect population dynamics. Specifically, we evaluate changes in turnover of discrete breeding patches within the colony, age structure and breeding performance and. Once predators entered the colony, the number of occupied patches increased, indicating a higher turnover patch; breeders responded behaviourally by moving eastwards to less accessible areas to predators. More importantly from a demographic point of view, presence of predators caused differential breeding dispersal by experienced, better performing breeders being more prone to leave the colony. This differential dispersal modified the age structure and reduced the reproductive value of the population. The role of non-lethal effects for population dynamics might be more important than previously thought, especially under scenarios of global change that predict increases in magnitude and frequency of perturbations, such as invasive predators.

Key-words:Predators presence, seabirds, invasive, non-lethal effects

4.2 Introduction

Humans have deeply transformed the planet and there is virtually no pristine environment left (Walther et al. 2002). Our activities have altered natural ecosystems so much that previously rare and extreme events are more frequent and intense than they used to be (Boyce et al. 2006). We have promoted unprecedented species movement facilitating both native and alien species to become invaders (Wanless et al. 2007, Carey et al. 2012). For instance, changes in socioeconomic features have led to increases in mesopredator abundances leading to declining prey populations, sometimes destabilizing communities and driving local extinctions (Prugh et al. 2009). Ecological responses of plant and animal populations to such changes are already visible (Walther et al. 2002). Animal populations — and individuals within them — respond to perturbations in two non-exclusive ways: by adjusting their behaviour, phenology, breeding and/or foraging ecology to survive and reproduce within the same areas and/or modifying their spatial distribution (Boyce et al. 2006, Gremillet and Boulinier 2009). Perturbations can drive, therefore, population changes by influencing individuals vital rates through both lethal and/or non-lethal effects (Boyce et al. 2006). Over the last recent decades, lethal effects of perturbations — i.e. direct mortality — have been thoroughly studied in wild animal populations (Loss et al. 2015). For instance, invasive species have driven numerous animal and plant populations to extinction (Clavero and Garcia-Berthou 2005), or extreme climatic events, such as heat waves, can cause species extirpation and changes at community and ecosystem level (Wernberg et al. 2016). Non-lethal effects of perturbations such as dispersal have been also studied but mainly focusing on species distribution changes (Wikenros et al. 2016).

Seabirds have been commonly used as a biological model to assess the lethal effects of some types of perturbations (Lewison et al. 2004, Croxall et al. 2012). For instance, during the last decades devastating effects of predators introduction by humans in previously free predator areas has been linked to the decline and/or the extirpation of numerous native animal populations worldwide (Wanless et al. 2007, Cresswell 2008, Fernandez-Chacon et al. 2013). This is particularly true for numerous seabird species evolved in predator-free environments and lacking of appropriate behavioural responses (Igual et al. 2007, Wanless et al. 2007). Philopatry has evolved as an advantageous strategy for many species, benefiting from increased knowledge about their environment (Greenwood and Harvey 1982, Cresswell 2008, Milot et al. 2008). However, from an evolutionary point of view, vagility of some organisms (such as birds, bats or fish) should allow them to respond to perturbations such as predators presence by dispersing to other patches and, therefore, to avoid lethal effects of predation (Fernandez-Chacon et al. 2013, Mikula et al. 2016, Munsch et al. 2016). When presence of predators causes strong disturbance, (e.g. by reducing breeding success) behavioural responses such as dispersal should appear (Wanless et al. 2007, Cresswell 2008, Fernandez-Chacon et al. 2013). Interestingly, it has been recently suggested that individuals might respond differently in the face of perturbations depending on their previous experience, showing innovative behaviours, such as changes in migration patterns or colonization of new environments (Teitelbaum et al. 2016)(Payo-Payo et al. 2017). In that cases, experience-dependent behavioural responses can potentially result into shifts in the population age-structure and reproductive value — fitness of long-lived species usually increases with age, reaching its maximum value in intermediate ages — modifying populations ability to respond to perturbations (Sanz-Aguilar et al. 2008, Oro et al. 2013b, Payo-Payo et al. 2016). Here, we explore potential non-lethal effects of a mesocarnivores invasion at a previously free-predator colony of Audouin's gull (*Ichthyaetus audouinii*) (BirdLife Int). In the early 1980s, this gull species colonized the Ebro Delta; the number of breeding individuals progressively increased to a dynamic equilibrium regime in the early 2000s; and from mid-2000s breeding population has been steadily declining (Fernandez-Chacon et al. 2013). The causes underlying population decrease remain unclear, but it has been suggested to be a consequence of the non-lethal effects of density dependence and intense perturbation regime — such as appearance of predators and extreme weather events — which included dispersal to other colonies and settlement of new colonies by adults and experienced breeders (Fernandez-Chacon et al. 2013, Payo-Payo et al. 2017).

Since the species is vagile but exhibits philopatric behaviour we expect to identify resilient mechanisms to cope with predators such as changes in the spatial distribution of breeding patches within the colony (Cam et al. 2004, Igual et al. 2007, Oro et al. 2011). Previous studies suggest that more experienced individuals are more competent in dealing with environmental change (Teitelbaum et al. 2016, Payo-Payo et al. 2017) Therefore, we also hypothesize that under the scenario of decreasing population size and if predators presence promotes age-dependent behavioural responses — leading to breeding dispersal of experienced birds — younger, and inexperienced breeders should occupy the perturbed habitat in higher proportions (Fernandez-Chacon et al. 2013, Payo-Payo et al. 2017). Such increase in the proportion of younger individuals should then lead to knock-off effects on breeding performance, potentially influencing egg volume, clutch size and/or breeding success.

4.3 Material and methods

4.3.1 Species and the study area

The Audouin's gull is an endemic Mediterranean seabird (Oro and Ruxton 2001). Since 1981, the species most important colony located at Ebro Delta (40°37′ N, 00°35′ E) has been annually monitored and a mark-capture-recapture program is still ongoing, with more than 33000 individuals marked. Until the mid-2000s the colony hosted 70% of the species world population; however, from 2002 the population started to decline (Fernandez-Chacon et al. 2013, Payo-Payo et al. 2017).

Presence of alien mesopredators was first reported in 1994, but from 1997 mesopredators were regularly present at the breeding colony. Breeding individuals in the colony are spatially aggregated in discrete dunes and dikes (thereafter patches) (Genovart et al. 2003). Patches located at the eastern part of the colony — human managed saltplans — are usually surrounded by water and, therefore, more protected from predator presence, while those located at the western part of the colony — unmanaged dune vegetation — are not. Ebro Delta Natural Park Environmental Agency staff performs systematic surveys to detect carnivores annually. We used this information to define two different proxies: First, a qualitative presence proxy distinguishing before (< 1997) and after (≥ 1997) predators presence was regular and a quantitative abundance proxy accounting for the number of mesopredators present in the study area in a given year. These two proxies allowed us to assess the non-lethal effects of predators presence in three different population traits: spatio-temporal distribution of breeding patches, age structure and breeding performance (Payo-Payo et al. 2017).

4.3.2 Spatio-temporal distribution of breeding patches

Patch's occupation is registered every year, which allowed us to record the number of occupied patches (N), occupation of new patches (N_{col}) and patch extinctions (N_{ext}). By means of a GLM we quantitatively assessed if presence and/or abundance of predators in the colony had an effect on any of the three variables (N, N_{col}, N_{ext}). N_{col} and N_{ext} models accounted for the number of active colonies the same and the previous year, respectively. In addition to this, we assessed the effects of predators' presence in the distribution of breeding patches by looking at the temporal evolution of patch spatial distribution (Fig 12) and then quantitatively by comparing two lineal models (no effect vs temporal trend) on the distance of the breeding area centroid to the easternmost point of the breeding colony. We calculated breeding area centroid as mean position of breeding patches weighted by the number of pairs breeding in each patch.

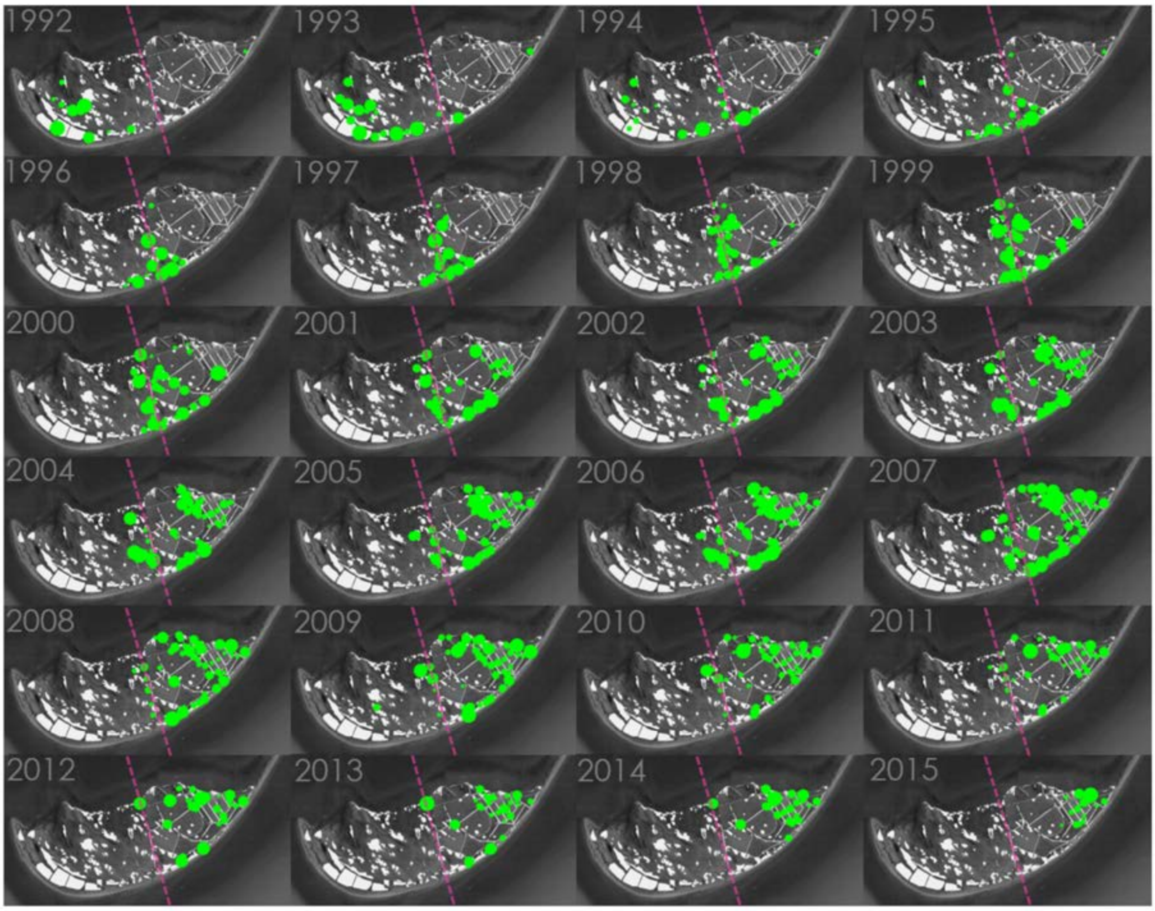

Fig. 12: White polygons represent the spatial distribution of potentially suitable breeding areas. Each annual image covers $60km^2$. Green circles represent approximated location of occupied patches and circle size is proportional to the number of individuals breeding in each patch. Predators were regularly present in the colony from 1997. Purple dashed line represents the interphase between unmanaged dune vegetation (left) and human managed saltplans (right). Maps modified from: Google, 2016 DigitalGlobe using R (Team 2013).

4.3.3 Age structure

Audouin's gulls usually recruit at the age of 3 or 4 and we assumed full recruitment at age 6 (Oro and Pradel 2000). Since age is a good indicator of breeding experience, we considered individuals between 3-5 years old as young and inexperienced breeders (YB). Determining the age structure of the population is a difficult task because age of breeders ($\geq 3 years old$) in this gull species cannot be assessed morphologically. Moreover, the proportion of marked individuals of different ages alive depends on numbers of fledglings marked by cohort and their subsequent survival. Therefore, we assumed that individuals experienced age dependent survival and that recapture of breeders within the study area is age independent (Payo-Payo et al. 2016). Under these assumptions, we consider that changes in the difference between the observed and expected proportion of young and inexperienced individuals (3-5 years old) are a good proxy of changes in age structure ($CDIF_t$) resulting from non-random dispersal. We used a total of 14113 resights of marked known-age gulls during the breeding period (April-June) to calculate the annual number of observed individuals of each age class. The annual number of expected individuals of age 'a' at time 't' was estimated following Eq.4.1. For instance, the expected number for individuals of age 3 at time 4 ($N_{3,4}$) would be number of chicks tagged at t=1 (M_1) that survived to t=4 ($N_{3,4} = M_1\Phi_1\Phi_2\Phi_3$). We calculated the annual proportions of observed and expected young and inexperienced breeders (YBOt and YBEt, respectively, see Appendix D.2.3) following Eq.4.2 (i.e. dividing the sum of young and inexperienced breeders,

$$\sum_{a=3}^{a=5} N_{a,t}$$

; by the total number of breeders,

$$\sum_{a=3}^{a=23} N_{a,t}$$

. For instance, the proportion of young and inexperienced breeders (3-5 years old) for time 4 would then be $N_{3,4} + N_{4,4} + N_{5,4})/N_{3-23,4}$. Finally, we calculated the annual difference between the observed and the expected annual proportions of young and inexperienced breeders as a proxy of age structure (Eq. 4.3). Positive $CDIF_t$ values will indicate an excess in the proportion of young and inexperienced breeders (or equivalently a lack of experienced breeders) compared to what we expected under the assumptions of our study.

$$N_{a,t} = M_{a,t} \prod_{a=1}^{a} \Phi_a \tag{4.1}$$

$$YB_t = \frac{\sum_{a=3}^{a=5} N_{a,t}}{\sum_{a=3}^{a=23} N_{a,t}} \tag{4.2}$$

$$CDIF_t = \frac{YBO_t}{YBE_t} \tag{4.3}$$

Finally, by means of a lineal model we tested for the effect of the annual number of predators in age structure ($CDIF_t$).

4.3.4 Breeding performance

We tested for effects of presence and intensity of predation on egg volume (Egg Vol), clutch size (CS) and breeding success (BS) between 1992 and 2015. We used linear models to test effects on CS and BS, and general linear models including nest identity as a random factor to test Egg Vol differences. Additionally, we tested for the presence of a linear relationship between patch breeding success and age structure of all patches in a given year (2012). We also collected data on breeding success of new formation colonies for qualitative comparation with our study colony (Sant Antoni $40^{\circ}43'22.8''N$, $0^{\circ}52'11.78''E$; La Ràpita $40^{\circ}37'0.50''N$, $0^{\circ}36'19.29''E$ and Castellón, 39°57′49.40”N, $0^{\circ}0'34.98''E$)(Payo-Payo et al. 2017).

Analyses were implemented in R software and models were selected using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Further details of data collection on each one of the variables are in Appendix D.1.

4.4 Results

Presence of predators caused increases rates of patch occupation (Fig. 13.a). Breeders responded to predator presence by moving eastwards ($\backsim 180m/y$, $R^2 = 0.79$, $p - value < 0.001$) towards patches surrounded by water, therefore less accessible to predators (Fig. 13.b and Fig. 12, Appendix D.2, Video D.2.2 and Tables 20 and 21. Neither presence nor abundance of predators triggered immediate colonization or extinction of new patches (see Appendix D.2, Table 20).

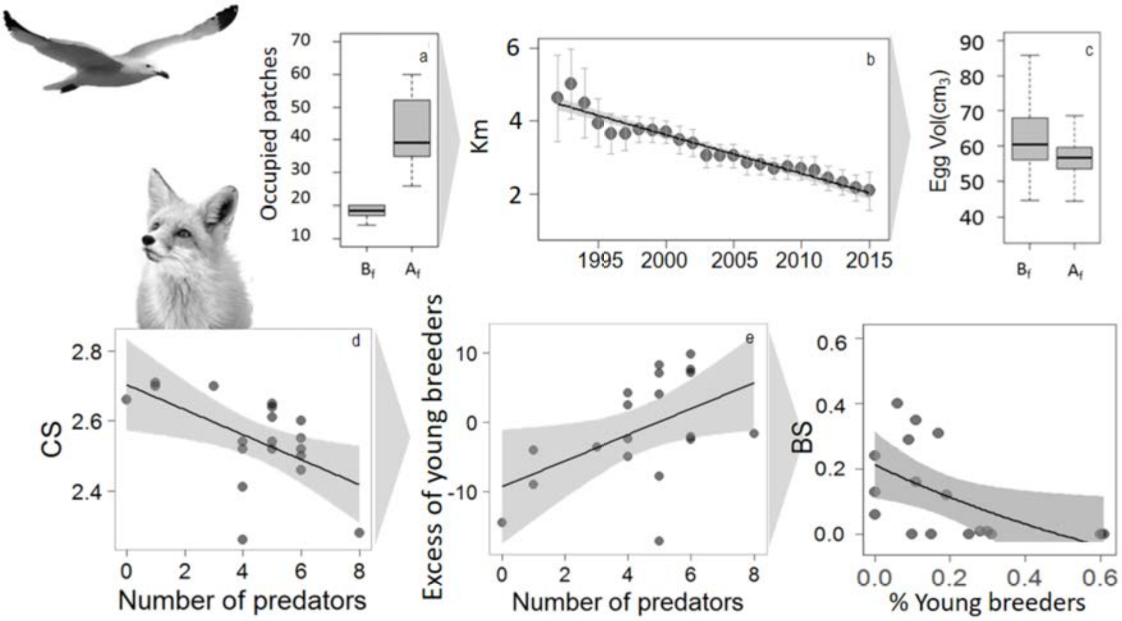

Fig. 13: Changes in patch occupation (a), temporal evolution (1992-2015) of the mean distance (1.96 SE) between the breeding area centroid and the eastermost point of the Ebro Delta colony (40.59 N, 0.71 E). (b), egg volume, Egg Vol (c) before, B_f and after, A_f predators entered the colony. Mean clutch size, CS (d) and excess of young and inexperienced breeders in relation with number of predators (relative difference between the observed and expected young and experienced breeders, positive numbers indicate lower proportions of experienced breeders as expected). Example of the year 2012 for the relationship between breeding success and % of young breeders (f). Fox modified from photo 'Redfox10'. (c) Cadigan. 2014:`<https://flic.kr/p/kFvEbZ>`. The image can be used under a CC by 2.0 `<https://creativecommons.org/licenses/by/2.0/>`

The difference between the expected and the observed proportion of young and inexperienced breeders was positively correlated with the number of predators present at the colony ($R^2 = 0.33$, $F_{1,21} = 10.55$, $p - value = 0.004$). Egg volume was lower after predators entered the study area (Figure 13.c and Appendix D.2, Table 21-20. Clutch size was negatively correlated with the number of predators (Fig. 14.d and Appendix D.2, Tables 21-20). Breeding success in the different patches in 2012 was negatively correlated with the proportion of young and inexperienced breeders in each of the patches (Fig. 13.f and Appendix D.2, Tables 21-20). Breeding success decreased during the study period (Fig. 14, $R^2 = 0.48$, $F_{1,15} = 15.64$, $p - value = 0.001$) and it was lower at la Banya than in any other breeding colony with no predators (Fig 14).

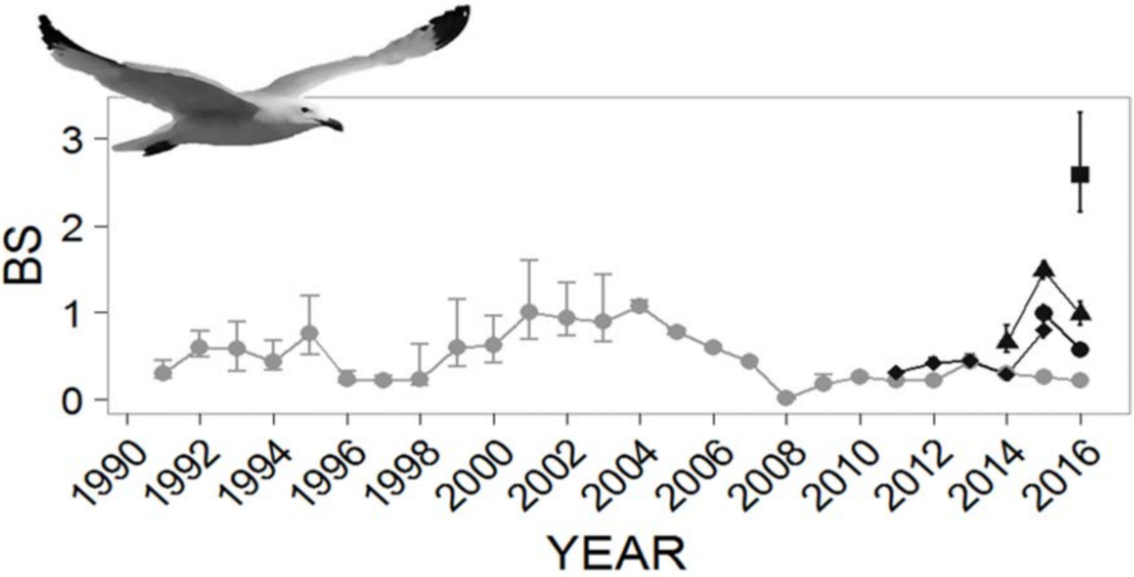

Fig. 14: Breeding success (chicks/pair) and standard error of different Audouin's gull breeding colonies: Punta de la Banya (light grey circles), La Ràpita (diamonds), Sant Antoni (triangles) and Castellón (squares).

4.5 Discussion

Our results suggest that non-lethal effects of density-independent perturbations such as the appearance of predators can drive changes in populations age structure and consequently, in reproductive value. Moreover, our results confirm previous evidences indicating that the underlying mechanism driving the spatial scale of dispersal is experience (Payo-Payo et al. 2017). Non-lethal effects — such as behavioural responses — seem to be more important than previously thought for population dynamics and might have key implications in how populations respond to perturbations.

Philopatry is a common phenomenon among vertebrates and many species usually benefit of familiarity with the environment when conditions are relatively predictable (Greenwood 1980). However, when environmental variability increases, behavioural responses such as dispersal are crucial to respond to perturbations (Slatkin 1987, Payo-Payo et al. 2017, Gilpin 2012). Previous studies in the same area, reported for the first time in the literature, a large scale non-random dispersal process (10 - 100 km), resulting in the occupation of predator-free patches and severe population consequences (Fernandez-Chacon et al. 2013, Payo-Payo et al. 2017). Here, we also identified dispersal movements at small spatial-temporal scale ($< 1km/y$). Patch occupation turnover within the studied area resulted in the displacement of breeding patches towards areas less accessible to predators (Payo-Payo et al. 2017). Patch occupation turnover is likely a resilient mechanisms to face mesopredator presence and to avoid the inherent risks of long-distance dispersal (Oro et al. 2009, Payo-Payo et al. 2017). Previous studies in the same colony showed that some of those patches with lower mesopredator accessibility experienced higher breeding success(Payo-Payo et al. 2017). However, overall breeding success in the studied colony decreased during the study period. Several possible and nonexclusive hypotheses have been usually proposed to explain changes in breeding success across taxa. First, low food availability, low parental condition and high density-dependence during the breeding period are usually linked to decreases in individual and population breeding success (Atkinson and Ramsay 1995, Coulson et al. 2000, Leaper et al. 2006). For instance, southern right whale (*Eubalaena australis*) populations experience enhanced breeding success when environmental conditions are favourable for krill growth (Leaper et al. 2006); female polar bears (*Ursus marinus*) show low body condition and breeding success after prolonged fasting or ungulates — such as Saiga antelope (*Saiga tatarica tatarica*), Soay sheep (*Ovis aries*) and Red deer (Cervus elaphus) — experienced depressed fecundity rates under high population densities (Atkinson and Ramsay 1995, Coulson et al. 2000, Leaper et al. 2006). Second, predator vigilance, alarm, avoidance, escape, and defence behaviours can reduce breeding success through increased physiological stress, reduce foraging efficiency or diminished parental care as shown in a wide range of taxa such as birds, snow-shoe hares, arctic ground squirrels or elks (Boonstra et al. 1998, Karels et al. 2000, Creel et al. 2007, Cresswell 2008). Third, populations experiencing presence of predators can also experience reduced breeding success through direct brood consumption (Oro 1998, Martínez-Abraín et al. 2012). For instance, roseate terns (*Sterna dougalii*) abandoned the breeding site after 24% of eggs and 77% of their chicks were depredated by corvids and gulls; introduced brown (*Salmo trutta*) and rainbow (*Onchorhynchus mykiss*) trouts caused decreases of spotted tree frog (*Litoria spenceri*) larval survival and contributed to populations' decline in south-eastern Australia; or wolves predating on ungulate population show preference for young of the year consumption during the summer (Pimlott 1967, Whittam and Leonard 1999, Gillespie 2001) .

Here, we propose a new density-independent mechanism explaining the decrease in the overall population breeding success. Our results are in agreement with recent research on birds population, which states that population dynamics seem to be primarily driven by density-independent recruitment at small population sizes, whereas close to their carrying capacity, they are driven by density-dependent mortality (Saether et al. 2016). Similar findings have been shown for ungulates, whose recruitment is both density-dependent and density-independent and adult survival is usually buffered against variation (Gaillard et al. 1998). Our results suggest that predators' presence is driving changes in population age structure (i.e. proportions of experienced breeders are decreasing) and therefore in the population reproductive value. Fitness of long-lived species usually increases with age, reaching its maximum value in intermediate ages (Sanz-Aguilar et al. 2008, Oro et al. 2013b). Previous studies in the study area revealed that site fidelity was the most common strategy among breeders, however, breeding site can be abandoned after a series of cumulative perturbations (Cam et al. 2004, Fernandez-Chacon et al. 2013). Moreover, it has been recently discovered that establishment of new sites and innovative responses to environmental change are driven by experience (Teitelbaum et al. 2016). We suggest that experienced breeders are the ones endeavouring large-scale dispersal and that this non-random dispersal is causing changes in the population age structure (Payo-Payo et al. 2017). This might be also link to another underlying mechanism, relaxed competition for limited breeding sites would have also favoured recruitment of competitively inferior individuals' (i.e. young or inexperienced breeders). The difference between the observed and expected proportion of young breeders was positively correlated with the number of predators and the proportion of young breeders in the population was negatively correlated with breeding success. Therefore, we suggest that perturbations can also drive changes in the reproductive value of the population through selection for young and inexperienced breeders with lower breeding success (Oro et al. 2013b). Moreover, resilience and philopatry seem to result in non-linear relationships between colonisation of new patches and adverse breeding conditions. Such seems to be in agreement with previous findings, experienced breeders act as an information repository which is extremely valuable when making risk-taking decisions in the face of perturbations (Teitelbaum et al. 2016, Payo-Payo et al. 2017).

In summary, we show that non-lethal effects of perturbations such as non-random dispersal carry large population trade-offs which might be larger than lethal effects themselves (Creel and Christianson 2008). Experience seems a valuable resource to overcome uncertainty and appears to drive the gradient between small and large scale dispersal in the face of perturbations. Our work emphasizes that it is not safe to assume that behavioural responses have no or limited effects on population dynamics and such effects should be accounted for in population modelling. Our results emphasize the importance of carefully considering the role of non-lethal effects and experience seems to be more important than previously thought, especially under scenarios of global change that predict increases in magnitude and frequency of perturbations.

III | Epilogue

General discussion

The importance of long-term and large scale monitoring

The overarching aim of my thesis was to assess the role of environmental variability and specially of perturbations in the population dynamics of social vertebrates. For this to be meaningful, it was critical to assess population responses across broad scales of space (local-global) and time (9-30y). The temporal dimension of population dynamics has historically received more attention than population fluctuations over space (Oro 2013). Collecting both spatially structured and long term population data require an enormous effort, but understanding population processes requires a complete perspective of both of their spatial and temporal dimensions (Tilman 1997). The four studies (Chapters) presented here intended to typify the spatio-temporal complexity of environmental conditions, and aimed to provide an approximation to a wide range of population responses. It would have been impossible to address the questions explored in this thesis if it wasn't for the effort of the Population Ecology Group (GEP) to maintain the life-histories monitoring — despite logistic and economic constrains — of individuals for decades (Mills et al. 2015). Therefore, my thesis emphasizes the need to collect individual, population and metapopulation data at long term and large spatial scales.

Bringing data, theory and modelling together

New insights in the understanding of the ecological responses to environmental variability and perturbations can only arise from the interaction between long-term and large-scale empirical data and theory through the use of ecological modelling (Bascompte and Solé 1998b). My results also emphasize the use of models that simplify complexity and concentrate on reproducing specific population processes to describe new patterns and to test hypotheses (Bascompte and Solé 1998a). Early ecologists faced numerous methodological limitations which prevented them from fully understanding some processes. Probably, due to these limitations their theoretical understanding of ecology was deeper than ours — it is certainly deeper than mine — but they seldom had the data to test their hypotheses and if they had it, they sometimes lacked the appropriate methods to analyse it. Today's methodological advances make possible to process the information underlying long-term and large-scale multivariate data series. Sometimes such advances appear disconnected from ecology, and despite combining theory, data and modelling is exciting, it is also challenging.

For instance, using long data series provides a rare opportunity to address interesting questions; however, they are likely to exhibit non-stationary dynamics making the interpretation of results difficult (Hanski 1999). Besides, models are no more than an abstraction — a subjective construction — based on our previous knowledge of the system; therefore, they are not necessarily right or wrong, they are just useful or not (Almaráz 2014). Here, I have attempted to counter balance these three assets: ecological modelling, theory and empirical data. Theory and models used here intend to represent the state of the art in current ecology and the field studies and datasets I have worked with are rather unique. However, the great value of this thesis arises from their combination

Table 8: Description of the different case studies and the main biological questions addressed in this thesis.

Ch.	Sp	Temp. scale	Spat. scale	Biological question	Results
1	YLG	Short (9y)	Local (Majorca)	What are the consequences of consecutive perturbations on the trophic ecology, survival and population size of an overabundant generalist seabird species?	Food limitation triggered dispersal and poisoning caused additive mortality. Both processes were responsible for population control.
2	AG	Large (26y)	Large (Delta-Senegal)	Do harsh environmental conditions experienced by individuals during early life influence population dynamics? If present, do these effects fade with age?	First year survival decreased with stronger density dependence and harsh climate. Consecutive cohort effects represent a selection filter.
3	AG	Large (30y)	Medium (W Med)	Do adverse breeding conditions trigger colonisation? Does personal information play an important role in colonisation? Do colonisers experience greater fitness?	Colonisations are temporally and spatially unpredictable and respond to an accumulation of perturbations. Colonisers are experienced breeders and colonisation results in increased breeding success.
4	AG	Large (23y)	Small (Delta)	Can non-lethal density independent perturbations such as predation drive changes in population dynamics?	Individuals responded by moving to less accessible areas. Presence of predators caused non-random dispersal, modified age structure and reproductive value of the population.

which allowed us to contribute to the understanding how and why populations fluctuate in natural ecosystems (Oro 2013).

Understanding the mechanisms driving population regulation and species distributions are two fundamental questions in ecological research (Tujlapurkar and Caswell 1997). Originally laboratory experiments were used to test specific hypotheses about the responses of populations to different perturbations, but they failed to solve the challenge of understanding population fluctuations in a holistic manner (Oro 2013). To fully understand such processes it is necessary to study natural populations (Oro 2013). Populations have resilient properties that allow them to persist after perturbations, but they can also crash and collapse following extreme values of environmental and demographic stochasticity or due to deterministic factors (Oro 2013). While small local populations can eventually go extinct, the whole metapopulation may persist, even in a rapidly changing world, because dispersal allows for the recolonization of empty patches and colonisation of new ones (Cappuccino 1995, Hutchings 2000, Oro 2013, Elias-Wolff et al. 2016). In this context, my thesis provides new information about different mechanisms operating in wild populations after perturbations.

Effects of environmental variability and consecutive perturbations

As expected for long-lived species, perturbations encouraged species to halt breeding investment in order to ensure future survival (Saether et al. 1996). For instance, sudden termination of supplementary feeding caused a significant decrease in breeding performance (clutch size and egg volume) of YLG breeding in Dragonera colony (Chapter 1) (Steigerwald et al. 2015). Likewise, predator presence also caused a decrease in breeding success of Audouin's gulls breeding at Ebro Delta (Chapter 3 and 4). However, under severe perturbation regimes an unknown resilience threshold was surpassed and foregoing reproduction was insufficient to buffer population changes (Myers et al. 1997, Solé 2007). For instance, after two consecutive perturbations – termination of PAFS and an inadvertent poisoning event — their synergic or cumulative effects lead to an important reduction in YLG population size (Chapter 1). Similar pattern was detected in Ebro Delta where the combined effect of an intense perturbation regime — climatic stochasticity and predator presence — and density dependence (Chapter 2, 3 and 4) seem to have caused the decline of the previously most important breeding site for the Audouin's gull in the western Mediterranean.

Despite this thesis does not have a direct interest in conservation biology, some or my results can also inform management actions. Programs aiming to control so-called overabundant species are often based in enacting direct culling which has been shown to be expensive and have little or no effect on scavengers' population numbers (Baker and Harris 2006, Oro and Martínez-Abraín 2007, Warburton and Norton 2009). Probably because resilient mechanisms — such as earlier recruitment or density-dependent higher fertility and immigration — were likely enhanced by high food availability (Brooks and Lebreton 2001, Oro and Martínez-Abraín 2007). Long-term limitation of resources seem to be relevant to controlling overabundant species by reducing recruitment (Oro and Martínez-Abraín 2007). Cumulative perturbations seem to magnify population decreases across different spatio-temporal scales through differential individual responses (i.e. non-random dispersal) and they might be useful when aiming to control so-called overabundant species. Since long-term consequences of consecutive perturbations are unknown; caution must be taken when implementing such measures. For instance, intense Yellow-legged gull culling at Medes Islands caused massive dispersal towards Ebro Delta where the species competed with and predated on more sensible species (Bosch et al. 2000).

Differential individual responses

This thesis provides evidences of how perturbations induced differential individual responses and we suggest that these differential responses are the ultimate mechanism underlying population decreases. For instance, individuals showed differential responses depending on their cohort of birth, quality, age and experience. Such differential responses represent a structuring force — potentially stabilizing population dynamics (Tujlapurkar and Caswell 1997).

In Chapter 2 we showed that harsh early-life conditions, both during rearing and first winter, strongly influence first-year survival but that influence was different among cohorts of birth — individuals born under favourable conditions survived better and it was not consistent through the individuals' life — it faded at older ages. Therefore, individuals differ considerably in their future performance depending on their life stage and cohort of birth and these variations can act as a structuring force in population dynamics (Beckerman et al. 2002, Benton et al. 2006). Interestingly, we were not able to detect cohort effects beyond the second year of life, however we present evidences from the same study area suggesting that older/more experienced individuals are dispersing and colonizing new environments (Chapters 3 and 4). Our analyses focused on cohort effects on local survival, therefore they do not consider dispersal and it is possible that non-random dispersal is masking potential cohort effects in older age classes.

We also showed differences in responses to perturbations depending on the individuals' quality. In Chapter 1 we detected how the termination of PAFS decreased the carrying capacity of the system and triggered a diet shift towards marine resources and increased resource competition. As expected, individuals experienced decreases in breeding performance, but they also suffered decreases in body mass and local survival. Similar pattern was observed in other species such as kittiwakes (*Rissa tridacryla*) breeding in Shetland when experiencing low food availability (Oro and Furness 2002). PAFS are especially beneficial for individuals with of low quality or reproductive value (Gremillet et al. 2008, Oro et al. 2013a, Steigerwald et al. 2015). Thus, the effects of food limitation, together with the inadvented poisoning event, were likely to have been more severe in low quality individuals — experiencing mortality, than in high quality individuals — which might have responded by dispersing (Steigerwald et al. 2015). In Chapter 2 we detected a similar pattern and both rearing and first winter periods seem to be operating as severe selection filter likely resulting in a positive selection for high-quality phenotypes and leading to stabilization of adult survival at high values by environmental canalization (Stearns 1992, Gaillard et al. 1998, Monaghan 2008, Sergio et al. 2011, Kendall et al. 2011)). Since selection was more intense in those age classes least capable to cope with adverse environmental conditions, our results emphasize the need to monitor early life stages to understand how they respond to perturbations and environmental variability (Sanz-Aguilar et al. 2012, Sergio et al. 2014).

Ageing is often accompanied by gradual within-individual improvements (Sergio et al. 2014). Therefore, age or experience are also reliable indicators of individual quality (Sergio et al. 2011, Teitelbaum et al. 2016). In fact, in Chapters 3 and 4 we explore the differential responses of experienced (i.e. older) individuals in the face of perturbations. Our results suggest that experienced individuals act as an information repository which is extremely valuable when making risk-taking decisions in the face of perturbations (McComb et al. 2001, Teitelbaum et al. 2016). Experienced individuals are more likely to endeavour long-term dispersal movements and to colonize new environments (Chapter 3 and 4). In my opinion this is the most exciting finding of this thesis, because it provides new insights to explain recent questions in population ecology. First, differential individual responses to non-lethal perturbations resulted in changes in population age structure and breeding success, through the dispersal of older and experienced individuals with higher breeding success (Hernandez et al. 2016). This result lead to the formulation of a new density-independent mechanism explaining decreases in the overall population breeding success (Chapter 4). Second, we show that non-lethal effects of perturbations such as non-random dispersal carry large population effects which might be larger than lethal effects themselves (Creel and Christianson 2008). Third, our results emphasize the need for accounting for individual heterogeneity in population modelling (Gimenez and Choquet 2010). Traditional interpretation of population and metapopulation dynamics assumes that all individuals interact equally with each other and with the environment (Hanski 1999). In many cases this simplification is an acceptable approximation, in some other cases it is not (Hanski 1999). Population models should account for the higher demographic value of experienced breeders since metapopulation dynamics might be more sensitive to those individuals than previously thought. Finally, these results are also relevant in terms of population responses to global change. Populations that include older, more experienced, individuals are expected be more likely to effectively and rapidly adapt to environmental change, at least in long lived, social species that exhibit social learning (Slatkin 1987, Gilpin 2012).

Non-linearity in population responses

There was an overall trend for environmental variability and perturbations to induce complex delayed responses and lead to covariance processes within demographic traits across different spatio-temporal scales. We demonstrate here that both density-dependent processes — such as food limitation — and density-independent processes — such as poisoning, predator presence or climatic conditions — can shape population dynamics through changes on breeding performance, survival, dispersal or age structure.

The effects of density-dependence on population dynamics and population regulation have been a hot topic in ecology for decades (May et al. 1974, Fowler 1987, Oro et al. 2006). Our results emphasize the need to acknowledge that when density-dependent mechanisms operate through resource competition the use of 'resource availability per capita' appears as a more accurate proxy to assess their effects.

Our results also evidence the existence of delayed effects, such as variability and delay in density dependence responses in population dynamics (Chapter 1, 2 and 3) or dispersal (Chapter 1, 3 and 4) and delayed colonization (Chapter 3). We still lack sound understanding of population functioning and their responses to environmental variability and perturbations. The results presented here should also make us reconsider some of the biases we suffer when interpreting nature with a narrow ecological time perspective. For instance, the biology of social vertebrates is among the most studied topics in the fields of ecology and evolution (Clutton-Brock et al. 1987, Schreiber and Burger 2001, Gill 2007). This fact reflects the long tradition of comparative work on their life-history characteristics which has influenced a great deal of early and current thinking in the study of ecology. Specifically, extensive work has been developed to understand Audouin's gull biology. However, it seems that we still fail to completely understand its ecology.

In the early 80s' Audouin's gull was considered a specialist species with very low behavioural plasticity (Oro et al. 1997). Here, we have shown that organisms respond to environmental variation and perturbations both immediately and over time. Despite some populations might be in the way to become marginal or even extinct, the species shows innovative responses — such as colonization of natural and anthropogenic environments — and its metapopulation seem to be able to persist and respond to severe perturbations by shifting its spatial distribution. Metapopulation persistence suggests that the time lags observed between the perturbations and population responses must be within the natural time scale of the system, therefore they seem to be acting as stabilizing mechanisms (May et al. 1974).

Such findings are particularly relevant to understand how population respond to consecutive perturbations, for instance under scenarios of global change that predict increases in their magnitude and frequency (Katz et al. 2005, Emanuel 2005, Boyce et al. 2006). Populations will be more likely to face the spatio-temporal overlap of perturbations effects. Furthermore, populations will also face the ovelap of such perturbations with the environmental policies aiming to mitigate their impacts (Bicknell et al. 2013, Oro et al. 2013a). Emendations to the European Landfil Waste or the Common Fisheries Directives constitute a unique opportunity to assess delayed and non-lineal population responses to perturbations and environmental variability (Benton et al. 2006, European-Commission 2008, E.U. 2009, Bicknell et al. 2013, European-Commission 2014) . However, while aiming for healthier ecosystems they might pose immediate challenges for the persistence of wild populations (Bicknell et al. 2013).

Overall, in this thesis we evaluated the effects of environmental variability and perturbations across different spatio-temporal scales. All the results here reported provide useful evidence-based information for population and metapopulation modelling. Specifically, we provide strong evidences showing that consecutive perturbations, non-lethal effects and non-random individuals' responses across different life stages are more important than previously thought. These results are especially relevant for understanding how populations will respond to the predicted increases in magnitude and frequency of perturbations as a consequence of global change.

General conclusions

1. This thesis emphasizes the need to collect individual, population and metapopulation data at long term and large spatial scales. Such information is crucial to understand wild animal populations respond to environmental variability and perturbations.
2. Here, we demonstrate that environmental variability and perturbations induce complex responses and lead to covariance processes within demographic traits at different spatio-temporal scales.
3. As expected for long-lived species, perturbations encouraged species to halt breeding investment in order to ensure future survival. However, under strong perturbation regimes the population resilience threshold is surpassed.
4. Cumulative effects of perturbations magnified population decreases across large spatio-temporal scales. Consecutive perturbations are potentially useful tools to effectively manage overabundant species. However, caution must be taken because individuals can disperse.
5. Severe environmental conditions caused both lethal and non-lethal responses on populations. Non-lethal responses include changes in foraging behaviour, development cultural innovations such non-random dispersal movements or colonization of novel environments.
6. Individuals responded differentially to environmental variability and consecutive perturbations depending on their individual quality, age and experience. Such differential responses resulted in severe selection filters and represent a structuring force — potentially destabilizing population dynamics.
7. Processes underlying the strong early-life selection pressures on early life survival are not limited to the rearing period, first winter is also critical. Consecutive cohort effects driven by density dependence and climate influence early-life survival of long-lived species, but that influence faded at older ages.
8. Experienced individuals act as an information repository. They are more likely to engage large distance dispersal and colonize new environments. Populations that include older individuals are more likely to be able to effectively and rapidly adapt to environmental change, at least in long lived, social species that exhibit social learning.
9. Colonisations are temporally and spatially unpredictable and respond to an accumulation of perturbations exceeding an unknown threshold for colonising new patches. The temporal mismatch between perturbations and colonisations events suggests that colonisers need a longer prospecting period to compensate for the lack of public information.
10. Non-lethal, density independent perturbations, such as predators' presence, can drive changes in populations age structure and, therefore in the population reproductive value, through selection for young and inexperienced individuals with lower breeding success.

11. We provide strong evidences showing that consecutive perturbations, non-lethal effects and non-random individuals' responses across different life stages are more important than previously thought. These results are especially relevant for understanding how populations will respond to the predicted increases in magnitude and frequency of perturbations as a consequence of global change.

Discussión general (Castellano)

La importancia del control de poblaciones a grandes escalas espacio temporales

El objetivo general de la tesis era evaluar el papel de la variabilidad ambiental y en particular de las perturbaciones en la dinámica poblacional de las aves marinas. Para que esto tuviera sentido, era fundamental evaluar las respuestas poblacionales a lo largo de grandes escalas espacio (local-global) temporales (9-30 años). La dimensión temporal de la dinámica poblacional históricamente ha recibido más atención que las variaciones espaciales (Oro 2013). Recoger datos que capten la estructura espacial de las poblaciones a largo plazo requiere un esfuerzo enorme, sin embargo, entender los procesos que tienen lugar en las poblaciones requiere una visión completa de ambas dimensiones (espacio y tiempo) (Tilman 1997). Los cuatro estudios (capítulos) presentados en esta tesis tipifican la complejidad espacio-temporal de las condiciones ambientales, y pretenden dar una aproximación de un amplio rango de respuestas poblacionales. Habría sido imposible explorar las preguntas planteadas en esta tesis si no fuera por el esfuerzo del Grupo de Ecología de Poblaciones (GEP) por mantener el estudio de las historias de vida individuales durante décadas — a pesar de las limitaciones logísticas y económicas (Mills et al. 2015). Por lo tanto, mi tesis enfatiza la necesidad de recoger datos individuales, poblacionales y metapoblacionales a grandes escalas espacio–temporales.

Conectando datos, teoría y modelado

Avances en el conocimiento de las respuestas ecológicas a la variabilidad ambiental y las perturbaciones sólo pueden surgir de la interacción entre datos a gran escala espacio temporal y la teoría ecológica, a través del modelado ecológico (Bascompte and Solé 1998b). Mis resultados enfatizan el uso de modelos que simplifican la complejidad y concentran sus esfuerzos en reproducir respuestas poblacionales específicas para describir patrones y testar hipótesis (Bascompte and Solé 1998a). Los ecólogos pioneros se enfrentaron a numerosas limitaciones metodológicas que impidieron que entendieran completamente algunos procesos. Probablemente, debido a dichas limitaciones su entendimiento de la teoría ecológica era más profundo que la nuestra — desde luego es más profundo que el mía — pero en ocasiones no contaban con los datos o los métodos apropiados para comprobar sus hipótesis. Los avances metodológicos actuales hacen posible procesar la información subyacente en las grandes series multivariantes de datos espacio-temporales. En ocasiones dichos avances parecen estar desconectados de la ecología ya que a pesar de que combinar teoría, datos y modelado es apasionantes, también supone un gran reto.

Por ejemplo, usar series de datos temporales largas proporciona una oportunidad excepcional para explorar preguntas interesantes; sin embargo, son muy proclives a presentar dinámicas no estacionarias haciendo difícil la interpretación de resultados (Hanski 1999). Además, los modelos no son más que una abstracción — una construcción subjetiva— basada en nuestro conocimiento previo del sistema; por lo tanto, no son necesariamente correctos o incorrectos, sino útiles o no (Almaráz 2014). Aquí, he intentado combinar

Table 9: Descripción de los diferentes casos de estudio y de las principales preguntas ecol'ogicas exploradas en la tesis.

Cap	Sp	Escala temp	Escala. esp.	Pregunta	Resultado
1	YLG	Corta (9a)	Local (Mallorca)	¿Cuáles son las consecuencias de las perturbaciones consecutivas en la ecología trófica, la supervivencia y el tamañ poblacional de una especie de ave marina generalista	La falta de alimento causó dispersión y el envenenamiento causó mortalidad aditiva. Ambos procesos fueron responsables del control poblacional.
2	AG	Larga (26a)	Larga (Delta-Senegal)	¿Las condiciones ambientales durante las etapas tempranas de vida pueden influenciar la dinámica de poblaciones? Si es así, ¿Dicho efecto desaparece con la edad?	La supervivencia durante el primer año de vida disminuyó como consecuencia de la denso-dependencia y de las condiciones climáticas adversas. Ambos efectos representan un filtro de selección.
3	AG	Larga (30a)	Media (O Med)	¿Pueden las condiciones adversas durante la cría desencadenar colonizaciones? ¿Cuál es el papel de la información privada en las colonizaciones? ¿Los colonizadores experimentan mayor eficiencia ecológica?	Las colonizaciones son espacial y temporalmente impredecibles y responden a la acumulación de perturbaciones. Los colonizadores son reproductores experimentados y la colonización resulta en mayor éxito reproductor.
4	AG	Larga (23a)	Pequeña (Delta)	¿Pueden los efectos no letales de perturbaciones denso-independientes como la presencia de predadores dar lugar a cambios en la dinámica de poblaciones?	Los individuos responden moviendose a áreas menos accesibles. La presencia de predadores causa dispersión no aleatoria, modificó la estructura de edad y el valor reproductor de la población.

estos tres aspectos: modelado ecológico, teorá y datos emprícos. La teoría y los modelos usados en esta tesis intentan ser una representación del estado del arte en ecología moderna y los estudios de campo, así como los datos derivados de ellos, son únicos. Sin embargo, el valor de esta tesis surge de su combinación, la cuál nos ha permitido contribuir al entendimiento de cómo y por qué las poblaciones varian en los sistemas naturales (Oro 2013).

Entender los mecanismos que regulan la abundancia y distribución de las poblaciones son dos de las preguntas fundamentales en la investigación ecológica (Tujlapurkar and Caswell 1997). Originariamente los experimentos de laboratorio se usaban para comprobar hipótesis especficas sobre las respuestas poblacionales a diferentes perturbaciones, pero a menudo fallaban al intentar entender cómo las poblaciones fluctúan en un contexto más holístico (Oro 2013). Para entender completamente dichos procesos es necesario estudiar las poblaciones naturales (Oro 2013). Las poblaciones tienen propiedades resilientes que les permiten persistir después de las perturbaciones, pero también pueden colapsar después de valores extremos de variabilidad ambiental, estocasticidad demográfica o debido a factores determinísticos (Oro 2013). Mientras que pequeñas poblaciones pueden desaparecer, la metapoblación puede persistir, incluso en un ambiente que cambia rápidamente, ya que la dispersión permite la recolonización de áreas desocupadas y la colonización de nuevos ambientes (Cappuccino 1995, Hutchings 2000, Oro 2013, Elias-Wolff et al. 2016). En este contexto, mi tesis proporciona nueva información sobre los diferentes mecanismos que operan en las poblaciones salvajes después de las perturbaciones.

Efectos de la variabilidad ambiental y las perturbaciones consecutivas

Como esperabamos para especies longevas, las perturbaciones promovieron la omisión de la reproducción para asegurar la supervivencia futura (Saether et al. 1996). Por ejemplo, la repentina desaparición de los subsidios alimentarios causó un descenso significativo en el éxito reproductor (tamaño de puesta y volumen de huevo) de las gaviotas patiamarillas que crían en Dragonera (Capítulo 1 Steigerwald et al. (2015)). De manera similar, la presencia de predadores causó una disminución en el éxito reproductor de las gaviotas de Audouin que crían en el Delta del Ebro(Captulos 3 y 4). Sin embargo, bajo régimenes de perturbaciones severos un umbral desconocido de resiliencia fue superado y saltarse la reproducción no fue suficiente para tamponar cambios poblacionales (Myers et al. 1997, Solé 2007). Por ejemplo, después de las dos perturbaciones consecutivas — desaparición de los subsidios alimentarios y el envenenamiento puntual— sus efectos sinérgicos y/o acumulados dio lugar a una drástica reducción de la población de gaviota patiamarilla (Capítulo 1). Detectamos un patrón similar en el Delta del Ebro donde el efecto combinado de un intenso régimen de perturbaciones — estocasticidad climática y presencia de predadores — y denso-dependencia (Capítulos 2, 3 y 4) parecen ser responsables del descenso poblacional en la que antes era la colonia de cría más importante para las gaviotas de Audouin en el Oeste del Mediterráneo.

A pesar de que esta tesis no tiene un interés directo en la biología de la conservación, algunos de mis resultados pueden ser utilizados para informaracciones de manejo. Los programas de control de especies denominadas como superabundantes suelen basarse en programas de descaste cuyos efectos en las poblaciones de especies carroñeras son pequeños o nulos (Baker and Harris 2006, Oro and Martínez-Abraín 2007, Warburton and Norton 2009). Probablemente porque diversos mecanismos resilientes — como por ejemplo, reclutamiento temprano o procesos densodependientes como alta fertilidad e inmigración — son promovidos por la alta disponibilidad de alimento (Brooks and Lebreton 2001, Oro and Martínez-Abraín 2007). La limitación de rescursos alimenticios a largo plazo parece ser relevante para controlar especies denominadas superabundantes a través del reclutamiento (Oro and Martínez-Abraín 2007). Los efectos acumulados de las perturbaciones parecen amplificar los descensos poblacionales a lo largo de diferentes escalas espacio-temporales a través de respuestas individuales diferenciales (p. e. dispersión no aleatoria)y por lo tanto pueden ser útiles para controlar las especies denominadas como superabundantes. Sin embargo, dado que las consecuencias a largo plazo de las perturbaciones son desconocidas; su aplicación debe realizarse con cautela. Por ejemplo, el descaste de gaviota patiamarilla realizado en las Islas Medas a finales de los años 90 dio lugar a dispersión masiva de individuos al Delta del Ebro donde la especie compite y depreda especies más sensibles (Bosch et al. 2000).

Respuestas individuales diferenciales

Esta tesis proporciona evidencias de como las perturbaciones promovieron respuestas individuales diferenciales y sugiere que dichas respuestas son el mecanismo subyacente al descenso poblacional. Por ejemplo, los individuos presentaron respuestas diferenciales dependiendo de la cohorte de nacimiento, la calidad individual, la edad y la experiencia. Dichas respuestas diferenciales representan una fuerza estructural — con potencial desestabilizador para la dinámica poblacional (Tujlapurkar and Caswell 1997).

En el capítulo 2 demostramos como las condiciones severas durante fases de vida temprana, durante el periodo cría y el primer invierno, tienen fuertes efectos sobre la supervivencia durante el primer año de vida pero dicha influencia fue diferente en función de la cohorte de nacimiento — aquellos individuos que experimentaron condiciones favorables durante las primeras etapas de vida sobrevivieron mejor y dicho efecto no fue consistente a lo largo de la vida del individuo — y se atenuó con la edad. Por lo tanto, los individuos presentan diferencias considerables en su respuesta en función de la etapa de vida y de la cohorte de nacimiento y dichas variaciones pueden actuar como una fuerza estructural en la dinámica de las poblaciones (Beckerman et al. 2002, Benton et al. 2006). Es interesante que no fuimos capaces de detectar efectos cohorte más allá del primer año de vida, sin embargo también presentamos evidencias de que los individuos que solían críar en esa misma área de estudio pero que son de mayor edad y más experimentados dispersan y colonizan nuevas áreas (capítulos 3 y 4). Nuestros análisis se centran en los efectos cohorte sobre la supervivencia local, por lo que no consideran la dispersión y es posible que la dispersión diferencial esté enmascarando posibles efectos cohorte en el resto de clases de edad.

Además, tambien mostramos diferencias en las respuestas de los individuos a las perturbaciones dependiendo de la calidad individual. En el capítulo detenctamos como la desaparición de los subsidios alimentarios de origen antrópico hizo descender la capacidad de carga del sistema y desencadeno un cambio de dieta hacia recursos marinos incrementado la competencia. Como esperabamos, los individuos más experimentaron descensos en el éxito reproductor pero también en el peso y la supervivencia local. Patrones similares han sido observado en otras especies como las gaviotas tridáctilas (*Rissa tridacryla*) que crían en Shetland (Oro and Furness 2002). PAFS are especially beneficial for individuals with of low quality or reproductive value (Gremillet et al. 2008, Oro et al. 2013a, Steigerwald et al. 2015). Los efectos de la limitación alimentaria, junto con el envenenamiento, fueron posiblemente más severos en individuos de baja calidad — experimentando mortalidad, que en individuos de alta calidad — los cuales probablemente respondieron dispersando (Steigerwald et al. 2015). En el capítulo 2 detectamos un patrń análogo, el periodo de cría y el primer invierno parecen operar como un filtro de selección severo que resulta en la selección positiva de individuos con fenotipos de mayor calidad y en la estabilización de la supervivencia adulta en valores altos debido a la canalización ambiental (Stearns 1992, Gaillard et al. 1998, Monaghan 2008, Sergio et al. 2011, Kendall et al. 2011) . Dado que la selección es más intensa en aquellas clases de edad que tienen menor capacidad para soportar condiciones ambientales adversas, nuestros resultados enfatizan la necesidad de controlar las fases de vida tempranas para entender como estas responden a las perturbaciones y a la variabilidad ambiental (Sanz-Aguilar et al. 2012, Sergio et al. 2014).

El envejecimiento a menudo va acompañado de mejoras graduales en los individuos (Sergio et al. 2014). Por lo tanto, la edad y la experiencia son indicadores fiables de la calidad individual (Sergio et al. 2011, Teitelbaum et al. 2016). De hecho, en los capítulos 3 y 4 exploramos las respuestas diferenciales de individuos reproductores más experimentados (de mayor edad)frente a las perturbaciones. Nuestros resultados sugieren que los individuos experimentados actúan como un repositorio de información que es extremadamente valioso en el momento de tomar decisiónes tras las perturbaciones (McComb et al. 2001, Teitelbaum et al. 2016). Los individuos experimentados son más proclives a llevar a cabo movimientos dispersivos a gran escala y a colonizar nuevos ambientes (Capítulos 3 y 4). En mi opinión este es el resultado más interesante de la tesis, ya que proporciona nuevos datos para explicar algunas de las preguntas actuales en ecología. En primer lugar, las respuestas individuales diferenciales a las perturbaciones resultaron en cambios en la estructura de edad y éxito reproductor, a través de la dispersión de individuos mayores y más experimentados con mayor éxito reproductor (Hernandez et al. 2016). Este resultado da lugar a la formulación de un nuevo mecanismo denso-independiente para explicar los descensos en el éxito reproductor (cápitulo 4). Segundo, mostramos que los efectos no letales de las perturbaciones como es la dispersión no aleatoria puede conllevar efectos en las poblaciones más importantes de lo que se pensaba previamente (Creel and Christianson 2008). Tercero, nuestros resultados enfatizan la necesidad de tener en cuenta la heterogeneidad individual en el modelado poblacional (Gimenez and Choquet 2010). La interpretación tradicional de la dinámica poblacional y metapoblacional asume que todos los individuos interactúan de igual manera entre ellos y con el medio que les rodea (Hanski 1999). En muchas ocasiones dicha simplificación es una aproximación aceptable pero en otros no lo es (Hanski 1999). Los modelos poblacionales deben tener en cuenta el mayor valor demográfico de los individuos reproductores experimentados ya que la dinámica metapoblacional parece ser más sensible a cambios en la proporción de dichos individuos de lo que antes se pensaba. Por último, estos resultados son también relevantes en el contexto del cambio global y las respuestas poblacionales a dichos cambios. Las poblaciones que incluyan individuos mayores o más experimentados probablemente tendrán mayor capacidad para adaptarse de manera más rápida y eficaz a cambios ambientales, al menos en especies sociales que presentan aprendizaje social (Slatkin 1987, Gilpin 2012).

Respuestas poblacionales no lineales

La variabilidad ambiental y las perturbaciones generaron de manera generalizada respuestas complejas y desfasadas, además dieron lugar a procesos de covarianza entre los distintos rasgos a diferentes escalas espacio-temporales. Demostramos que tanto los procesos denso-dependientes — como por ejemplo la limitación de recursos alimentarios — como los procesos denso-independientes — como el envenenamiento, la presencia de predadores y las condiciones climáticas — pueden tener efectos en la dinámica de poblaciones a través de cambios en el éxito reproductor, la supervivencia, la dispersión o la estructura de edad.

Los efectos denso-dependientes en la dinámica de poblaciones y en la regulación de las poblaciones han sido un tema de debate para los ecólogos durante décadas (May et al. 1974, Fowler 1987, Oro et al. 2006). Nuestros resultados enfatizan la necesidad de considerar que cuando los mecanismos denso-dependientes operan a través de procesos de competencia por recursos el uso de 'disponibilidad de recurso per capita' es un indicador más fiable de sus efectos.

Nuestros resultados también evidencian la existencia de efectos desfasados, como la variabilidad y desfase en las respuestas poblacionales denso-dependientes en la dinámica de poblaciones (Chapter 1,2 and 3) or dispersal (Capítulos 1,3y 4) y colonizaciones desfasadas en el tiempo (Capítulo 3). Aún fallamos al intentar comprender como las poblaciones fluctúan y de qué dependen sus respuestas a la variabilidad ambiental y las perturbaciones. Los resultados presentados aquí también deberían hacernos reconsiderar algunos de los sesgos que experimentamos cuando interpretamos la naturaleza sin la perspectiva temporal y ecológica adecuada. Por ejemplo, la biología, ecología y evolución de los vertebrados sociales ha sido estudiada de manera exhaustiva a lo largo de la historia (Clutton-Brock et al. 1987, Schreiber and Burger 2001, Gill 2007). Este hecho refleja una larga tradición de estudios comparativos sobre sus rasgos de vida y que ha influenciado gran parte del pensamiento ecológico actual. En particular, se han realizado muchisimo trabajo para entender la biología de especies como la gaviota de Audouin. Sin embargo, parece que aún no somos capaces de entender su ecología por completo. A principios de los años 80 la gaviota de Aduouin era considerada una especie especialista con baja plasticidad comportamental (Oro et al. 1997). Aquí, hemos demostrado que los organismos responden a las perturbaciones tanto de manera inmediata como a lo largo del tiempo. A pesar de que algunas poblaciones parezcan estar al borde del colapso, la especie presenta respuestas inovadoras — como la colonización de nuevos ambientes naturales y antropogénicos — y su metapoblación parece haber ser capaz de persistir y responder a régimenes de perturbaciones severos cambiando su distribución espacial. La persistencia de la metapoblación sugiere que los desfases temporales observados entre las perturbaciones y las respuestas poblacionales deben ocurrir dentro de la escala temporal del sistema, y parecen actuar como mecanismos estabilizadores (May et al. 1974).

Dichos resultados son particularmente relevantes para entender como las poblaciones responden a las perturbaciones consecutivas, por ejemplo en escenarios de cambio global que predicen incrementos en la magnitud y frecuencia de las perturbaciones (Katz et al. 2005, Emanuel 2005, Boyce et al. 2006).

Las poblaciones se enfrentaran con mayor frecuencia a el solapamiento espacio-temporal de las perturbaciones. Además, las poblaciones deberán enfrentarse a las consecuencias de las medidas ambientales que tienen como objeto reducir el impacto de las perturbaciones de origen antrópico (Bicknell et al. 2013, Oro et al. 2013a). Las enmiendas a la Política de Residuos Urbanos o a la Politica Pesquera Europea constituyen una oportunidad única para evaluar los desfases y respuestas no lineales de las poblaciones a las perturbaciones y a la variabilidad ambiental (Benton et al. 2006, European-Commission 2008, E.U. 2009, Bicknell et al. 2013, European-Commission 2014). Sin embargo, a la vez que pretenden favorecer la regenereración de ecosistemas más saludables pueden suponer diferentes retos para la persistencia de las poblaciones naturales (Bicknell et al. 2013).

En conclusión, esta tesis evalua los efectos de la variabilidad ambiental y las perturbaciones en poblaciones naturales a diferentes escalas espacio-temporales. Todos los resultados mostrados proporcionan información útil para el modelado poblacional y metapoblacional. En particular, proporcionamos fuertes evidencias que demuestran que las perturbaciones consecutivas, los efectos no letales y las respuestas diferenciales de los individuos a lo largo de las distintas etapas de la vida son más importantes de lo que se pensaba anteriormente. Estos resultados son especialmente releavantes para entender como las poblaciones naturales responderán a los incrementos previstos en la magnitud y la frecuencia de las perturbaciones como consecuencia del cambio global.

Conclusiones generales (Castellano)

1. Esta tesis enfatiza la necesidad de recoger datos a nivel individual, poblacional y metapoblacional a grandes escalas espaciales y temporales. Dicha información es crucial para entender como las poblaciones animales salvajes responderan a la variabilidad ambiental y las perturbaciones.
2. Aquí, demostramos que la variabilidad ambiental y las perturbaciones inducen respuestas complejas y dan lugar a procesos de covarianza entre diferentes rasgos vitales y a diferente escalas espaciotemporales.
3. Como se espera para las especies longevas, frente a las perturbaciones estas responden saltándose la reproducción antes que comprometer su supervivencia. Sin embargo, bajo régimenes de perturbaciones fuertes la resiliencia de la población puede verse comprometida.
4. Los efectos acumulados de las perturbaciones magnificaron los descensos poblacionales a diferentes escalas espacio temporales. Las perturbaciones consecutivas son potencialmente útiles para el control y manejo de especies sobreabundantes. Sin embargo, dichas medidas deben aplicarse con cuidado ya que los individuos pueden dispersar.
5. Condiciones ambientales severas causaron respuestas letales y no letales en las poblaciones. Las respuestas no letales incluyen cambios en el comportamiento de búsqueda de comida, desarrollo de innovaciones culturales como movimientos dispersivos no aleatorios o colonización de nuevos ambientes.
6. Los individuos respondieron de manera diferencial a la variabilidad ambiental y a las perturbaciones consecutivas dependiendo de su calidad individual, edad y experiencia. Dichas diferencias resultaron en severos filtros de seleccin y representan una fuerza estructural — desestabilizando potencialmente la dinámica de las poblaciones.
7. Los procesos subyacentes a las presiones de selección durante etapas de vida tempranas no se limitan al periodo de cría sino que el primer invierno también es crítico. La supervivencia se ve afectada por dos efectos cohorte consecutivos, resultado de la densodependencia y la influencia del clima durante etapas de vida tempranas, pero dicho efecto desaparece con la edad.
8. Los individuos experimentados actúan como un repositorio de información. Dichos individuos son más proclives a realizar grandes movimientos dispersivos y a colonizar nuevos ambientes. Es probable que las poblaciones que incluyen individuos mayores (edad) puedan adaptarse rápida y eficientemente a los cambios ambientales, al menos en especies longevas y sociales que presentan aprendizaje social.
9. La colonización de nuevos ambientes es espacial y temporalmente impredecible y ocurre una vez se ha superado un umbral tras a la acumulación de perturbaciones. El desajuste temporal entre las perturbaciones y las colonizaciones sugiere que los colonizadores requieren un periodo de prospección más largo para compensar la falta de información pública.

10. Perturbaciones no letales y denso–independientes, como por ejemplo la presencia de depredadores, puede dar lugar a cambios en la estructura de edad de las poblaciones y desencadenar cambios en el valor reproductivo de la población a través de la selección de individuos jóvenes con bajo éxito reproductor.

11. Presentamos evidencias sólidas que demuestra que las perturbaciones consecutivas, los efectos no letales y las respuestas no aleatorias de los individuos en diferentes estadios vitales son más importantes de lo que se creía anteriormente. Estos resultados son especialmente relevantes para entender como las poblaciones responderán a los incrementos en magnitud e intensidad de los régimenes de perturbaciones como consecuencia del cambio global.

IV | References

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V | Appendicces

A

Appendix Chapter 1

A.1 Extended results

Table 10: Results from Isotope Signatures General Linear Modelling of Yellow legged gulls breeding at Dragonera Island.

$\delta^{15}N$	Fixed	M_1	M_2	M_3	M_4	M_5
	i	10.827	10.605	10.903	10.691	10.693
	$\beta_{LANDFILL}$	-	0.397	-	0.423	0.419
	β_{SEX}	-	-	-0.148	-0.193	-0.197
	$\beta_{LANDFILL:SEX}$	-	-	-	-	0.007
	Random					
	i	0.010	0.000	0.014	0.000	0.000
	$\beta_{RESIDUAL}$	0.846	0.827	0.851	0.830	0.843
$\delta^{13}C$	Fixed					
	i	-19.900	-20.008	-19.775	-19.887	-19.906
	$\beta_{LANDFILL}$	-	0.189	-	0.225	0.262
	β_{SEX}	-	-	-0.240	-0.269	-0.227
	$\beta_{LANDFILL:SEX}$	-	-	-	-	-0.074
	Random					
	i	0.000	0.000	0.000	0.000	0.000
	$\beta_{RESIDUAL}$	0.660	0.661	0.655	0.653	0.663
$\delta^{34}S$	Fixed					
	i	12.865	11.348	12.512	11.059	10.956
	$\beta_{LANDFILL}$	-	2.967	-	2.878	3.085
	β_{SEX}	-	-	0.689	0.652	0.883
	$\beta_{LANDFILL:SEX}$	-	-	-	-	-0.410
	Random					
	i	3.855	1.562	3.683	1.567	1.585
	$\beta_{RESIDUAL}$	6.168	6.172	6.155	6.158	6.246

Intercept (i) and slopes ($beta$) for the fixed: landfill ($\beta_{LANDFILL}$), sex (β_{SEX})and their interaction ($\beta_{LANDFILL:SEX}$) and random: year ($\beta_{RESIDUAL}$) effects on $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ stable isotope signatures. Models are noted as in Table 5.

B

Appendix Chapter 2

B.1 Infography

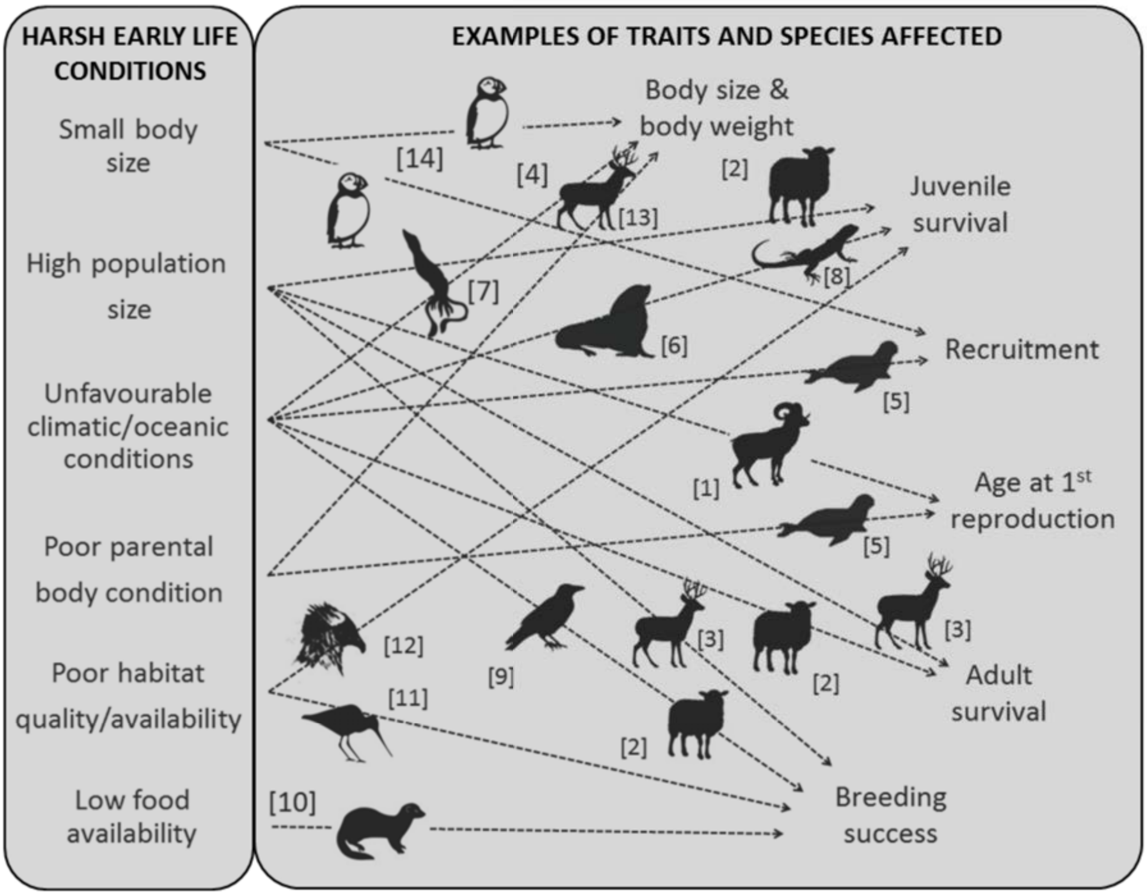

Fig. 15: Examples of early life conditions and the species and traits they have been reported to affect

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B.2 GoF Results

Results of the sum of the goodness-of-fit for Audouin's gulls breeding in the Ebro Delta. Results of the sum of the goodness-of-fit (GoF) tests of a general capture-recapture-recovery multistate (CMRR) model for each cohort of Audouin's gull. χ^2, Test value; df, degrees of freedom; $\hat{c}$, inflation factor, i.e. χ^2/df. The GOF component 3G SR tests for the presence of transients, i.e. individuals that are marked and are never recaptured or resighted; M.ITEC component tests for the presence of trap-dependence; and 'final $\hat{c}$' shows the overdispersion coefficient after correcting for these trap-dependence and transient effects in the starting models run in E-SURGE. 3G SM and LTEC have no direct biological interpretation but this test components are as in (Pradel et al. 2003, Oro et al. 2010).

Table 11: Goodness of fit tests for Audouin's gulls breeding at Ebro Delta

Test	χ^2	df	$\hat{c}$
3G SR	942.69	184	5.12
3G SM	177.62	167	1.06
M.ITEC	738.73	224	3.30
LTEC	530.28	333	1.59
Final $\hat{c}$	1.42		

Results of the goodness of fit (GoF) tests for the general capture–recapture-recovery multistate (CMRR) model for Audouin's gulls breeding at Ebro Delta.Test components are listed as in Pradel et al. (2003) where 3G: Tests for transients presence and M. Tests for trap dependence;χ^2: χ^2 statistic; df: degrees of freedom; $\hat{c}$: inflation factor i.e., χ^2/df.

The goodness-of-fit test (GoF) of the Jolly Move model (Brownie et al. 1993) for multistate data was calculated using U-CARE 2.3.2 (Pradel et al. 2003, Brownie et al. 1993, Choquet et al. 2005). GOF allows the sources of heterogeneity (i.e. trap-dependence or transience Pradel et al. (2005) to be detected and it is then possible to incorporate such information into the departure model by increasing its complexity. The fit of the general model for Audouin's gull was poor and so we followed (Oro et al. 2010) and performed a separate GoF test for each cohort and then summed results of all tests. We detected a significant trap-dependence effect — unequal probabilities of being reencountered given the previous encountered/non-encountered state — that has been reported in previous analysis from the Audouin's gull dataset (e.g. Fernandez-Chacon et al. (2013)). To account for this effect and following (Pradel and Sanz-Aguilar 2012), we introduced two additional recapture states (trap-aware and trap-unaware) into our model by means of a second step included after survival, which allowed us to estimate transitions between the two recapture states. We also detected a significant transient effect — the unequal probability between 'new' and 'old' individuals of being reencountered at any given time — that was accounted for by allowing survival to differ between newly marked and previously marked birds (Pradel et al. 2005). After accounting for trap-dependence and transience, an acceptable variance inflation factor 1.42 was obtained and applied to all models constructed in E-SURGE (Pradel 2005, Choquet and Nogue 2010).

B.3 Model parameterization

Appendix S3: Model parameterization. Multievent models use three different kinds of parameters: initial state probabilities (Π, matrix 1), transition between states probabilities (Ψ, matrix 2), and event probabilities (B, matrix 3). In our study transition probabilities are decomposed into two consecutive steps: the first (Ψ_1, matrix 2.1) represents survival probabilities (ϕ) and the second (Ψ_2, matrix 2.2) recapture probabilities (p); event probabilities correspond to the recovery probability (λ).

(1)

$$\Pi = \begin{array}{c} \begin{array}{cccc} \text{Aa} & \text{Au} & \text{Dr} & \text{Dl} \end{array} \\ \left(\begin{array}{cccc} 1 & 0 & 1 & 0 \end{array} \right) \end{array}$$

(2)

$$\Psi = \Psi_1 + \Psi_2$$

(2.1)

$$\Psi_1 = \begin{array}{c|cccc|c} & \text{Aa} & \text{Au} & \text{Dr} & \text{Dl} & \\ & \phi & 0 & 1-\phi & 0 & \text{Aa} \\ & 0 & \phi & 1-\phi & 0 & \text{Au} \\ & 0 & 0 & 0 & 1 & \text{Dr} \\ & 0 & 0 & 0 & 1 & \text{Dl} \end{array}$$

(2.2)

$$\Psi_2 = \begin{array}{c|cccc|c} & \text{Aa} & \text{Au} & \text{Dr} & \text{Dl} & \\ & p & 1-p & 0 & 0 & \text{Aa} \\ & p & 1-p & 0 & 0 & \text{Au} \\ & 0 & 0 & 1 & 0 & \text{Dr} \\ & 0 & 0 & 0 & 1 & \text{Dl} \end{array}$$

(3)

$$B = \begin{array}{c|ccc|c} & 0 & 1 & 2 & \\ & 0 & 1 & 0 & \text{Aa} \\ & 1 & 0 & 0 & \text{Au} \\ & 1-\lambda & 0 & \lambda & \text{Dr} \\ & 1 & 0 & 0 & \text{Dl} \end{array}$$

B.4 Three-step procedure for selecting the best general model structure

To select the best general model structure in Audouin's gull, we followed a three step procedure.

STEP1: We first modelled the recapture probability. All models included a temporal effect and a trap-dependence effect. Since Audouin's gulls usually recruit at the age of three years and rarely visit the colony during their first year of life, we tested a model with three age classes (1^{st}, 2^{nd} & $\geq 3^{rd}$ year) against a model with two age classes.

STEP2: once the best recapture structure was retained we continued modelling the recovery probability and we tested whether or not there was any temporal variation).

STEP3: finally, we modelled survival. We tested for temporal variation and a set of different age structures until we achieved the best structure. We ensured optimality of the final model by changing the parameter order in the selection procedure (results not shown).

Table 12: Best-model structure three step selection process for Audouin's gulls breeding in the Ebro Delta.

STEP1: Best recapture structure

ϕ	p	λ	NP	DEV	$QAIC_c$	$\Delta QAIC_c$
t	A_3+t+W	t	73	137419	96920	0
t	A_2+t+W	t	72	140808	99305	3615

STEP2: Best recovery structure

ϕ	p	λ	NP	DEV	$QAIC_c$	$\Delta QAIC_c$
t	A_3+t+W	t	73	137419	96920	0
t	A_3+t+W	CST	52	137531	96957	37

STEP3: Best survival structure

ϕ	p	λ	NP	DEV	$QAIC_c$	$\Delta QAIC_c$
A_5*t	A_3+t+W	t	158	134527	95054	0
A_6*t	A_3+t+W	t	177	134480	95060	6
A_7*t	A_3+t+W	t	195	134447	95072	18
A_4*t	A_3+t+W	t	138	134628	95085	31
A_8*t	A_3+t+W	t	212	134421	95088	34
A_2*t	A_3+t+W	t	95	134756	95089	35
A_9*t	A_3+t+W	t	228	134394	95101	47
A_3*t	A_3+t+W	t	117	134715	95104	50
A+t	A_3+t+W	t	96	134972	95243	189
A.t	A_3+t+W	t	348	134263	95251	197
A_9+t	A_3+t+W	t	81	135039	95260	206
A_6+t	A_3+t+W	t	78	135061	95270	216
A_5+t	A_3+t+W	t	77	135070	95274	220
A_8+t	A_3+t+W	t	80	135078	95285	231
A_4+t	A_3+t+W	t	76	135102	95295	241
A_7+t	A_3+t+W	t	79	135095	95295	241
A_2+t	A_3+t+W	t	74	135144	95320	266
A_3+t	A_3+t+W	t	75	135240	95390	335
A	A_3+t+W	t	75	136199	96065	1011
A_9	A_3+t+W	t	60	136245	96067	1013
A_8	A_3+t+W	t	59	136271	96083	1029
A_7	A_3+t+W	t	58	136298	96100	1046
A_6	A_3+t+W	t	57	136304	96103	1049
A_5	A_3+t+W	t	56	136311	96106	1052
A_4	A_3+t+W	t	55	136342	96126	1071
A_3	A_3+t+W	t	54	136366	96141	1086
A_2	A_3+t+W	t	53	136371	96142	1088

STEP 1, best recapture (p) structure probability; STEP2, best recovery (λ) probability structure and STEP 3, best survival (ϕ) probability structure for Audouin's gulls breeding in the Ebro Delta. NP, number of parameters; DEV, deviance; QAICc, second-order corrected Akaike's information criterion; $\Delta QAIC_c$, $QAIC_c$ difference with the best model; A_n, n age classes considered; t, time; CST, constant; W, trap awareness; '+', additive effect; '$*$', interaction effect. The best age-structure model is shown in bold for each step. All models were run with E-SURGE (Pradel 2005, Choquet and Nogue 2010). $\hat{c} = 1.42$.

B.5 Models used for describing survival in ANODEV methods

Table 13: Models used for describing survival (ϕ). F refers to models including only fixed effects. Subscripts CST, T and COV refer to constant, temporal and covariate models, respectively. Modified from (Grosbois et al. 2008).

Label	Formulation	Description	Parameters to be estimated
F_{CST}	$f(\phi) = a$	Survival is constant over years	One constant parameter
F_T	$f(\phi) = a_i$	Survival varies over time	One distinct parameter (a_i) for each time interval i in the time series.
F_{COV}	$f(\phi) = a + b_j x_{ji}$	Survival is determined by a linear relationship with the covariate j.	One parameter (a) for the intercepts. One parameter (b_j) for the relationship with covariate x_j.

To assess the effects of environmental covariates on residual unexplained variation in survival we used $Ftest_{CST/CO/T}$ ANODEV statistic (Skalski et al. 1993):

$$F_{CST/COV/T} = \frac{\frac{Dev(F_{CST}) - Dev(F_{COV})}{J-1}}{\hat{c}}$$

where $\hat{c} = \frac{Dev(F_{COV}) - Dev(F_T)}{n-J}$, n is the number of survival estimates obtained from model F_T, and J is the number of parameters required to describe the relationship between survival and the focal climatic or environmental covariate. Details of the formulation of each F model are explained in detail in Table 13. The fraction of temporal variation explained by the environmental and climatic covariates was estimated as R^2_{Dev} following (Skalski 1996):

$$R^2_{Dev} = \frac{Dev(F_{CST}) - Dev(F_{COV})}{Dev(F_{CST}) - Dev(F_T)}$$

B.6 Parameter estimates

Table 14: Estimates from the selected model in Audouin's gull (ϕ $A_5{*}t, pA_3 + t + W$, λ t, as seen in Table 12).

		PARAMETER ESTIMATES			
Parameter	Trap-dependence	*Year*	Age	Estimate	SE
ϕ		*1988*	1	n.e	n.e
ϕ		*1989*	1	0.764	0.135
ϕ		*1990*	1	0.874	0.083
ϕ		*1991*	1	0.733	0.064
ϕ		*1992*	1	0.919	0.062
ϕ		*1993*	1	0.653	0.085
ϕ		*1994*	1	0.771	0.056
ϕ		*1995*	1	0.388	0.042
ϕ		*1996*	1	0.530	0.085
ϕ		*1997*	1	0.547	0.034
ϕ		*1998*	1	0.323	0.061
ϕ		*1999*	1	0.503	0.058
ϕ		*2000*	1	0.560	0.058
ϕ		*2001*	1	0.515	0.059
ϕ		*2002*	1	0.509	0.045
ϕ		*2003*	1	0.614	0.038
ϕ		*2004*	1	0.558	0.029
ϕ		*2005*	1	0.641	0.047
ϕ		*2006*	1	0.533	0.040
ϕ		*2007*	1	0.240	0.040
ϕ		*2008*	1	n.e	n.e
ϕ		*2009*	1	0.322	0.124
ϕ		*2010*	1	0.091	0.094
ϕ		*2011*	1	0.000	0.000
ϕ		*1989*	2	0.996	0.000
ϕ		*1990*	2	0.952	0.046
ϕ		*1991*	2	0.655	0.083
ϕ		*1992*	2	0.944	0.062
ϕ		*1993*	2	0.763	0.061
ϕ		*1994*	2	0.841	0.107
ϕ		*1995*	2	n.e	n.e
ϕ		*1996*	2	0.933	0.079
ϕ		*1997*	2	0.821	0.131
ϕ		*1998*	2	0.996	0.000
ϕ		*1999*	2	0.895	0.147
ϕ		*2000*	2	0.870	0.096
ϕ		*2001*	2	0.918	0.089
ϕ		*2002*	2	0.896	0.096
ϕ		*2003*	2	0.905	0.075
ϕ		*2004*	2	0.926	0.048
ϕ		*2005*	2	1.000	0.000

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		PARAMETER ESTIMATES			
Parameter	Trap-dependence	*Year*	Age	Estimate	SE
ϕ		*2006*	2	0.879	0.060
ϕ		*2007*	2	0.920	0.061
ϕ		*2008*	2	0.774	0.124
ϕ		*2009*	2	0.316	0.135
ϕ		*2010*	2	0.763	0.296
ϕ		*2011*	2	0.195	0.209
ϕ		*1989*	3	0.979	0.020
ϕ		*1990*	3	0.875	0.146
ϕ		*1991*	3	0.962	0.084
ϕ		*1992*	3	0.883	0.056
ϕ		*1993*	3	0.875	0.043
ϕ		*1994*	3	0.975	0.019
ϕ		*1995*	3	0.827	0.061
ϕ		*1996*	3	0.940	0.046
ϕ		*1997*	3	0.965	0.032
ϕ		*1998*	3	0.962	0.042
ϕ		*1999*	3	0.897	0.066
ϕ		*2000*	3	0.904	0.033
ϕ		*2001*	3	0.952	0.026
ϕ		*2002*	3	0.916	0.034
ϕ		*2003*	3	0.971	0.027
ϕ		*2004*	3	0.877	0.033
ϕ		*2005*	3	0.833	0.044
ϕ		*2006*	3	0.966	0.026
ϕ		*2007*	3	0.988	0.015
ϕ		*2008*	3	1.000	0.000
ϕ		*2009*	3	0.678	0.453
ϕ		*2010*	3	0.332	0.069
ϕ		*1990*	4	0.852	0.031
ϕ		*1991*	4	0.967	0.031
ϕ		*1992*	4	0.925	0.041
ϕ		*1993*	4	0.901	0.036
ϕ		*1994*	4	0.931	0.027
ϕ		*1995*	4	0.884	0.032
ϕ		*1996*	4	0.911	0.030
ϕ		*1997*	4	0.848	0.038
ϕ		*1998*	4	0.949	0.032
ϕ		*1999*	4	0.943	0.031
ϕ		*2000*	4	0.881	0.045
ϕ		*2001*	4	0.956	0.025
ϕ		*2002*	4	0.911	0.024
ϕ		*2003*	4	0.880	0.024
ϕ		*2004*	4	0.901	0.025
ϕ		*2005*	4	0.847	0.029
ϕ		*2006*	4	0.902	0.033
ϕ		*2007*	4	0.950	0.038
ϕ		*2008*	4	1.000	0.000

Continues on the next page.

PARAMETER ESTIMATES

Parameter	Trap-dependence	*Year*	Age	Estimate	SE
ϕ		*2009*	4	0.633	0.060
ϕ		*2010*	4	0.316	0.217
ϕ		*1991*	5	0.938	0.028
ϕ		*1992*	5	0.954	0.015
ϕ		*1993*	5	0.906	0.015
ϕ		*1994*	5	0.968	0.016
ϕ		*1995*	5	0.903	0.016
ϕ		*1996*	5	0.932	0.013
ϕ		*1997*	5	0.866	0.013
ϕ		*1998*	5	0.909	0.013
ϕ		*1999*	5	0.878	0.013
ϕ		*2000*	5	0.885	0.012
ϕ		*2001*	5	0.855	0.014
ϕ		*2002*	5	0.857	0.014
ϕ		*2003*	5	0.845	0.013
ϕ		*2004*	5	0.896	0.013
ϕ		*2005*	5	0.908	0.014
ϕ		*2006*	5	0.905	0.016
ϕ		*2007*	5	0.889	0.020
ϕ		*2008*	5	0.769	0.019
ϕ		*2009*	5	0.666	0.025
ϕ		*2010*	5	0.345	0.016
p	Trap-aware	*1988*	1	0.000	0.000
p	Trap-aware	*1989*	1	0.000	0.000
p	Trap-aware	*1990*	1	0.000	0.000
p	Trap-aware	*1991*	1	0.002	0.000
p	Trap-aware	*1992*	1	0.006	0.001
p	Trap-aware	*1993*	1	0.007	0.001
p	Trap-aware	*1994*	1	0.008	0.001
p	Trap-aware	*1995*	1	0.003	0.000
p	Trap-aware	*1996*	1	0.006	0.001
p	Trap-aware	*1997*	1	0.010	0.001
p	Trap-aware	*1998*	1	0.007	0.001
p	Trap-aware	*1999*	1	0.006	0.001
p	Trap-aware	*2000*	1	0.012	0.002
p	Trap-aware	*2001*	1	0.014	0.002
p	Trap-aware	*2002*	1	0.006	0.001
p	Trap-aware	*2003*	1	0.009	0.001
p	Trap-aware	*2004*	1	0.012	0.002
p	Trap-aware	*2005*	1	0.005	0.001
p	Trap-aware	*2006*	1	0.006	0.001
p	Trap-aware	*2007*	1	0.004	0.001
p	Trap-aware	*2008*	1	0.004	0.001
p	Trap-aware	*2009*	1	0.006	0.001
p	Trap-aware	*2010*	1	0.004	0.001
p	Trap-aware	*2011*	1	1.000	0.000
p	Trap-aware	*1989*	2	0.000	0.000

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PARAMETER ESTIMATES

Parameter	Trap-dependence	*Year*	Age	Estimate	SE
p	Trap-aware	*1990*	2	0.000	0.000
p	Trap-aware	*1991*	2	0.110	0.010
p	Trap-aware	*1992*	2	0.307	0.017
p	Trap-aware	*1993*	2	0.348	0.016
p	Trap-aware	*1994*	2	0.372	0.016
p	Trap-aware	*1995*	2	0.191	0.010
p	Trap-aware	*1996*	2	0.304	0.014
p	Trap-aware	*1997*	2	0.413	0.016
p	Trap-aware	*1998*	2	0.329	0.014
p	Trap-aware	*1999*	2	0.310	0.014
p	Trap-aware	*2000*	2	0.453	0.016
p	Trap-aware	*2001*	2	0.502	0.016
p	Trap-aware	*2002*	2	0.310	0.013
p	Trap-aware	*2003*	2	0.394	0.014
p	Trap-aware	*2004*	2	0.461	0.014
p	Trap-aware	*2005*	2	0.277	0.011
p	Trap-aware	*2006*	2	0.292	0.012
p	Trap-aware	*2007*	2	0.208	0.009
p	Trap-aware	*2008*	2	0.220	0.011
p	Trap-aware	*2009*	2	0.306	0.015
p	Trap-aware	*2010*	2	0.221	0.015
p	Trap-aware	*2011*	2	1.000	0.000
p	Trap-aware	*1990*	3	0.000	0.000
p	Trap-aware	*1991*	3	0.335	0.021
p	Trap-aware	*1992*	3	0.644	0.016
p	Trap-aware	*1993*	3	0.686	0.013
p	Trap-aware	*1994*	3	0.707	0.012
p	Trap-aware	*1995*	3	0.491	0.014
p	Trap-aware	*1996*	3	0.641	0.012
p	Trap-aware	*1997*	3	0.742	0.011
p	Trap-aware	*1998*	3	0.667	0.012
p	Trap-aware	*1999*	3	0.647	0.012
p	Trap-aware	*2000*	3	0.772	0.010
p	Trap-aware	*2001*	3	0.805	0.009
p	Trap-aware	*2002*	3	0.648	0.011
p	Trap-aware	*2003*	3	0.726	0.010
p	Trap-aware	*2004*	3	0.777	0.008
p	Trap-aware	*2005*	3	0.610	0.010
p	Trap-aware	*2006*	3	0.628	0.010
p	Trap-aware	*2007*	3	0.517	0.011
p	Trap-aware	*2008*	3	0.535	0.012
p	Trap-aware	*2009*	3	0.643	0.013
p	Trap-aware	*2010*	3	0.537	0.019
p	Trap-aware	*2011*	3	1.000	0.000
p	Trap-unaware	*1988*	1	0.000	0.000
p	Trap-unaware	*1989*	1	0.000	0.000
p	Trap-unaware	*1990*	1	0.000	0.000

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PARAMETER ESTIMATES					
Parameter	Trap-dependence	*Year*	Age	Estimate	SE
p	Trap-unaware	*1991*	1	0.001	0.000
p	Trap-unaware	*1992*	1	0.003	0.000
p	Trap-unaware	*1993*	1	0.003	0.000
p	Trap-unaware	*1994*	1	0.004	0.001
p	Trap-unaware	*1995*	1	0.001	0.000
p	Trap-unaware	*1996*	1	0.003	0.000
p	Trap-unaware	*1997*	1	0.004	0.001
p	Trap-unaware	*1998*	1	0.003	0.000
p	Trap-unaware	*1999*	1	0.003	0.000
p	Trap-unaware	*2000*	1	0.005	0.001
p	Trap-unaware	*2001*	1	0.006	0.001
p	Trap-unaware	*2002*	1	0.003	0.000
p	Trap-unaware	*2003*	1	0.004	0.001
p	Trap-unaware	*2004*	1	0.005	0.001
p	Trap-unaware	*2005*	1	0.002	0.000
p	Trap-unaware	*2006*	1	0.003	0.000
p	Trap-unaware	*2007*	1	0.002	0.000
p	Trap-unaware	*2008*	1	0.002	0.000
p	Trap-unaware	*2009*	1	0.003	0.000
p	Trap-unaware	*2010*	1	0.002	0.000
p	Trap-unaware	*2011*	1	1.000	0.000
p	Trap-unaware	*1989*	2	0.000	0.000
p	Trap-unaware	*1990*	2	0.000	0.000
p	Trap-unaware	*1991*	2	0.052	0.005
p	Trap-unaware	*1992*	2	0.163	0.010
p	Trap-unaware	*1993*	2	0.191	0.010
p	Trap-unaware	*1994*	2	0.207	0.011
p	Trap-unaware	*1995*	2	0.094	0.006
p	Trap-unaware	*1996*	2	0.162	0.008
p	Trap-unaware	*1997*	2	0.237	0.011
p	Trap-unaware	*1998*	2	0.178	0.009
p	Trap-unaware	*1999*	2	0.166	0.009
p	Trap-unaware	*2000*	2	0.268	0.012
p	Trap-unaware	*2001*	2	0.308	0.013
p	Trap-unaware	*2002*	2	0.166	0.008
p	Trap-unaware	*2003*	2	0.223	0.010
p	Trap-unaware	*2004*	2	0.274	0.011
p	Trap-unaware	*2005*	2	0.144	0.007
p	Trap-unaware	*2006*	2	0.154	0.007
p	Trap-unaware	*2007*	2	0.104	0.005
p	Trap-unaware	*2008*	2	0.111	0.006
p	Trap-unaware	*2009*	2	0.163	0.009
p	Trap-unaware	*2010*	2	0.111	0.008
p	Trap-unaware	*2011*	2	1.000	0.000
p	Trap-unaware	*1990*	3	0.000	0.000
p	Trap-unaware	*1991*	3	0.182	0.013
p	Trap-unaware	*1992*	3	0.443	0.016

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PARAMETER ESTIMATES

Parameter	Trap-dependence	*Year*	Age	Estimate	SE
p	Trap-unaware	*1993*	3	0.491	0.015
p	Trap-unaware	*1994*	3	0.516	0.014
p	Trap-unaware	*1995*	3	0.299	0.012
p	Trap-unaware	*1996*	3	0.441	0.013
p	Trap-unaware	*1997*	3	0.559	0.013
p	Trap-unaware	*1998*	3	0.469	0.013
p	Trap-unaware	*1999*	3	0.448	0.013
p	Trap-unaware	*2000*	3	0.599	0.013
p	Trap-unaware	*2001*	3	0.645	0.013
p	Trap-unaware	*2002*	3	0.448	0.013
p	Trap-unaware	*2003*	3	0.539	0.012
p	Trap-unaware	*2004*	3	0.606	0.012
p	Trap-unaware	*2005*	3	0.408	0.011
p	Trap-unaware	*2006*	3	0.427	0.011
p	Trap-unaware	*2007*	3	0.321	0.010
p	Trap-unaware	*2008*	3	0.337	0.011
p	Trap-unaware	*2009*	3	0.443	0.014
p	Trap-unaware	*2010*	3	0.338	0.017
p	Trap-unaware	*2011*	3	1.000	0.000
λ		*1989*	2	n.e	n.e
λ		*1990*	2	0.000	0.000
λ		*1991*	2	0.046	0.022
λ		*1992*	2	0.019	0.009
λ		*1993*	2	0.058	0.038
λ		*1994*	2	0.016	0.007
λ		*1995*	2	0.020	0.009
λ		*1996*	2	0.120	0.018
λ		*1997*	2	0.035	0.010
λ		*1998*	2	0.041	0.012
λ		*1999*	2	0.032	0.008
λ		*2000*	2	0.056	0.011
λ		*2001*	2	0.029	0.007
λ		*2002*	2	0.017	0.005
λ		*2003*	2	0.014	0.004
λ		*2004*	2	0.022	0.005
λ		*2005*	2	0.035	0.007
λ		*2006*	2	0.035	0.008
λ		*2007*	2	0.025	0.005
λ		*2008*	2	0.031	0.005
λ		*2009*	2	0.038	0.013
λ		*2010*	2	0.012	0.003
λ		*2011*	2	0.006	0.002
λ		*2012*	2	0.006	0.002

n.e. Not estimable.

Survival (ϕ), recapture (p) and recovery (λ) estimates and their standard error (SE) by time, age and trap-dependence (trap-aware and trap-unaware).

B.7 Model selection & ANODEV

Table 15: Models were based on the best previously selected recapture (p), recovery (λ) and survival (ϕ) probability structure for Audouin's gull ($\phi A_5{*}t$, $pA_3 + t + W$, λt, as seen in Appendix B.4, Table 12). We tested the interaction effect of covariates with age (5 age classes, A_5). NP, number of parameters; DEV, deviance; $QAIC_c$, second-order corrected Akaike's information criterion; $\Delta QAIC_c$, $QAIC_c$ difference from the best model; $F_{n,m}$, F-Fisher value; n and m degrees of freedom for the F-Fisher; R^2, percentage of survival explained by the corresponding covariate; t, time; C, cohort; CST, constant; DD, tonnes of fish landed by trawlers per capita;W_{NAO}, North Atlantic Oscillation index during the first winter of life; '+', additive effect; '$*$', interaction effect. Best model (in bold) estimates are available in Appendix B.6 Table 14.

	NP	DEV	$QAIC_c$	$\Delta QAIC_c$	n	m	$F_{n,m}$	R^2	p-value
$\phi\ A_5{*}t$	158	134527	95054	0					
$\phi\ A_5{*}C$	158	134655	95145	91					
$\phi\ A_5$ + C	79	135332	95463	409					
$\phi\ A_5$ CST	56	136311	96106	1052					
$\phi\ A_5{*}DD$	61	135706	95689	635	5	97	9.962	0.339	< 0.001
$\phi A_5{*}W_{NAO}$	61	136001	95898	844	5	97	4.074	0.174	0.002
$\phi A_5{*}DD + W_{NAO}$	66	135552	95592	538	10	92	6.807	0.425	< 0.001
$\phi A_5{*}DD + W_{NAO} + DD{*}W_{NAO}$	71	135426	95513	459	15	87	5.707	0.496	< 0.001

B.8 Beta estimates of Audouin's gull survival

Table 16: Beta estimates and their confidence interval of Audouin's gull survival by age (ϕA_n, where n is age class) for food availability per capita (DD) and first winter conditions (W_{NAO}) as seen in Appendix B.9. i, intercept, β, slope in the logit scale (95% CI in parenthesis); '+', additive effect and '$*$', interaction effect; M_n, model identification as in Appendix B.9, Table 12.

	DD			W_{NAO}			DD+W_{NAO}			DD+W_{NAO}+DD*W_{NAO}		
$\phi\ A_1$	M_1			M_2			M_3			M_4		
	i	0.628	(0.463,0.793)	i	0.595	(0.499,0.691)	i	0.597	(0.416,0.766)	i	0.578	(0.443,0.712)
	β_{DD}	0.625	(0.248,1.001)	$\beta_{W_{NAO}}$	0.463	(0.376,0.551)	β_{DD}	0.549	(0.123,0.970)	β_{DD}	0.485	(0.177,0.790)
							$\beta_{W_{NAO}}$	0.298	(0.180,0.416)	$\beta_{W_{NAO}}$	0.282	(0.161,0.402)
										$\beta_{DD*W_{NAO}}$	-0.082	(-0.052,0.217)
$\phi\ A_2$	M_5			M_6			M_7			M_8		
	i	2.381	(1.978,2.785)	i	2.373	(1.966,2.780)	i	2.378	(1.967,2.788)	i	2.371	(1.968,2.774)
	β_{DD}	-0.007	(-0.317,0.302)	$\beta_{W_{NAO}}$	0.061	(-0.0421,0.545)	β_{DD}	-0.03	(-0.431,0.369)	β_{DD}	-0.126	(-0.774,0.523)
							$\beta_{W_{NAO}}$	0.078	(-0.429,0.585)	$\beta_{W_{NAO}}$	0.044	(-0.468,0.556)
										$\beta_{DD*W_{NAO}}$	0.076	(-0.412,0.564)
$\phi\ A_3$	M_9			M_{10}			M_{11}			M_{12}		
	i	2.583	(2.299,2.867)	i	2.589	(2.310,2.863)	i	2.585	(2.306,2.865)	i	2.577	(2.297,2.857)
	β_{DD}	-0.02	(-0.458,0.418)	$\beta_{W_{NAO}}$	-0.082	(-0.413,0.248)	β_{DD}	-0.013	(-0.367,0.341)	β_{DD}	-0.078	(-0.548,0.391)
							$\beta_{W_{NAO}}$	-0.081	(-0.407,0.243)	$\beta_{W_{NAO}}$	-0.100	(-0.439,0.239)
										$\beta_{DD*W_{NAO}}$	0.061	(-0.311,0.434)
$\phi\ A_4$	M_{13}			M_{14}			M_{15}			M_{16}		
	i	2.319	(2.147,2.491)	i	2.327	(2.154,2.499)	i	2.327	(2.154,2.500)	i	2.324	(2.150,2.497)
	β_{DD}	-0.019	(-0.266,0.227)	$\beta_{W_{NAO}}$	0.203	(-0.004,0.411)	β_{DD}	-0.021	(-0.277,0.235)	β_{DD}	-0.072	(-0.371,0.227)
							$\beta_{W_{NAO}}$	0.202	(0.006,0.398)	$\beta_{W_{NAO}}$	0.161	(-0.064,0.385)
										$\beta_{DD*W_{NAO}}$	0.111	(-0.158,0.379)
$\phi\ A_5$	M_{17}			M_{18}			M_{19}			M_{20}		
	i	2.044	(1.991,2.097)	i	2.097	(2.042,2.153)	i	2.07	(2.013,2.127)	i	2.083	(2.024,2.14)
	β_{DD}	0.044	(0.015,0.073)	$\beta_{W_{NAO}}$	-0.016	(-0.062,0.029)	β_{DD}	0.071	(0.036,0.106)	β_{DD}	-0.034	(-0.116,0.048)
							$\beta_{W_{NAO}}$	-0.081	(-0.138,-0.024)	$\beta_{W_{NAO}}$	-0.127	(-0.193,-0.061)
										$\beta_{DD*W_{NAO}}$	0.081	(0.024,0.140)

B.9 ANODEV Models for Audouin's gulls breeding at Ebro Delta

Table 17: Summary of the models calculated for the temporal model ANODEV for Audouin's gulls breeding in the Ebro Delta ($\phi A_5 * t$, $pA_3 + t + W$, λt, see Appendix B.4 for model details). ϕA_n , survival at age n; NP, number of parameters; DEV, deviance; $QAIC_c$, second-order corrected Akaike's information criterion; $\Delta QAIC_c$, $QAIC_c$ difference with the best model; n and m, degrees of freedom for the F-Fisher; $F_{n,m}$, F-Fisher value; R^2, percentage of first-year survival explained by the corresponding covariate; M_n, model identification for Appendix B.6; t, time; CST, constant; DD; tones of trawler fleet catches per capita during rearing; W_{NAO}; North Atlantic Oscillation index in the first winter of life,'+', additive effect; '$*$', interaction effect. The best model is in bold. Survival beta estimates (confidence interval) for each covariate and age class are available in Appendix B.6.

	NP	DEV	$QAIC_c$	$\Delta QAIC_c$	n	m	$F_{n,m}$	R^2	p-value	M_n	
ϕA_1	ϕt	158	134527	95054	0						
	ϕCST	137	134802	95206	152						
	ϕDD	138	134664	95110	56	1	20	20.146	0.502	0.000	M_1
	$\phi\ W_{NAO}$	138	134671	95115	61	1	20	18.261	0.477	0.000	M_2
	ϕDD+ W_{NAO}	139	134631	95089	35	2	19	15.552	0.621	< 0.001	M_3
	ϕDD+ W_{NAO}+ $DD*W_{NAO}$	140	134629	95090	36	3	18	10.146	0.628	< 0.001	M_4
ϕA_2	ϕ t	158	134527	95054	17						
	ϕCST	137	134562	95037	0						
	ϕDD	138	134560	95037	0	1	20	1.176	0.056	0.292	M_5
	$\phi\ W_{NAO}$	138	134560	95037	0	1	20	1.243	0.059	0.278	M_6
	ϕDD+ W_{NAO}	139	134560	95039	2	2	19	0.597	0.059	0.560	M_7
	ϕDD+ $W_{NAO} + DD*W_{NAO}$	140	134560	95041	4	3	18	0.381	0.060	0.768	M_8
ϕA_3	ϕt	158	134527	95054	8						
	ϕCST	137	134576	95046	0						
	ϕDD	138	134576	95048	2	1	20	0.076	0.004	0.785	M_9
	$\phi\ W_{NAO}$	138	134575	95048	2	1	20	0.211	0.010	0.921	M_{10}
	$\phi DD + W_{NAO}$	139	134575	95050	4	2	19	0.160	0.017	0.853	M_{11}
	$+W_{NAO} + DD*W_{NAO}$	140	134575	95052	6	3	18	0.102	0.017	0.921	M_{12}
ϕA_4	ϕt	158	134527	95054	4						
	ϕCST	138	134581	95052	2						
	ϕDD	139	134580	95054	4	1	19	0.235	0.012	0.634	M_{13}
	$\phi\ W_{NAO}$	139	134576	95050	0	1	19	1.975	0.094	0.176	M_{14}
	$\phi DD + W_{NAO}$	140	134575	95052	2	2	18	1.132	0.112	0.344	M_{15}

Continues on the next page.

		NP	DEV	$QAIC_c$	$\Delta QAIC_c$	n	m	$F_{n,m}$	R^2	p-value	M_n
	$\phi DD + W_{NAO} + DD{*}W_{NAO}$	141	134574	95053	3	3	17	0.829	0.128	0.496	M_{16}
ϕA_5	ϕ t	158	134527	95054	0						
	ϕCST	139	134739	95165	111						
	ϕDD	140	134726	95158	104	1	18	1.155	0.060	0.297	M_{17}
	ϕW_{NAO}	140	134739	95167	113	1	18	0.010	0.001	0.921	M_{18}
	$\phi DD + W_{NAO}$	141	134714	95152	98	2	17	1.117	0.116	0.352	M_{19}
	$\phi DD + W_{NAO} + DD{*}W_{NAO}$	142	134705	95147	93	3	16	1.029	0.162	0.406	M_{20}

C

Appendix Chapter 3

C.1 Temporal evolution of Audouin's gull breeding colonies

Video 1: Temporal evolution of Audouin's gull breeding colonies along the western Mediterranean coast at regular time intervals between 1983 and 2014. Circle size is proportional to the number of colonizers in the year of colony foundation; anchors indicate colonies settled in port areas (See Table 7 for colony details). Video is available via: `<https://drive.google.com/open?id=0BzfbihtntuT0aTFnVXlBWHZ5SzA>`

C.2 Model selection

Table 18: COL_t: colony in time t (*source*/*new*); CST, constant; BS_{t-1}, previous season breeding status; DEV, deviance; AIC_c: corrected Akaike's information criterion; ΔAIC_c: AIC_c difference with the best model.

	Model	DEV	AIC_c	ΔAIC_c
COL_t	CST		117	0
COL_t	BS_{t-1}	-0.725	118.2	1.2

Table 19: V_{t-1} , egg volume, CS_{t-1}, clutch size; LD_{t-1}, laying date; CST, constant, COLONY, source or new colony; DEV, deviance; AIC_c: corrected Akaike's information criterion; ΔAIC_c: AIC_c difference with the best model. *Includes nest as a random effect.

	Model	DEV	AICc	ΔAIC_c
V_{t-1}	CST*	252	258	2
V_{t-1}	COLONY*	250	256	0
CS_{t-1}	CST	30	123	0
CS_{t-1}	COLONY	30	125	2
LD_{t-1}	CST	1506	212	0
LD_{t-1}	COLONY	1478	214	2

D

Appendix Chapter 4

D.1 Extended methodology

D.1.1 Predator presence surveys

Natural park staff develops systematic diurnal and nocturnal walks to detect tracks and locate and georeference burrows of potential predators (Fig.16. Foxes, *Vulpes vulpes*, badgers, *Meles meles*; Beech martens, *Martes foina*; least weasels, *Mustela nivalis*; otters, *Lutra lutra*; cats, *Felis catus* and dogs, *Canis familiaris*) through the breeding season.

Fig. 16: Otter (*Lutra lutra*), Beech marten (*Martes foina*), least weasel (*Mustela nivalis*), cat (*Felis catus*), dog (*Canis familiaris*), foxes (*Vulpes vulpes*) and badgers (*Meles meles*). Images were modified from the Flirck photos: 'Audouin's Gull'. (c) Birdwatching BCN. 2013: <https://flic.kr/p/e22P1e>. 'Red fox 10' (c) Cadigan. 2014: <https://flic.kr/p/kFvEbZ>. 'Badger'(c) Blg ashb. 2015: <https://flic.kr/p/r2bEQV>. Breech marten (c) Steinmarder. 2012: ¡https://flic.kr/p/cD4bry>. 'Least weasel' (c) Blg-ashb. 2015: <https://flic.kr/p/qYTkSb>. 'Otter'. Trimming. 2010: <https://flic.kr/p/8Qh6XN>. 'Cat' (c) Kamaljith. 2011: <https://flic.kr/p/9hGdy5>. Dog.(c) Cole. 2012:<https://flic.kr/p/brLXug>. Ebro Delta (c) Oro 2004 All images can be used under a CC by 2.0 <https://creativecommons.org/licenses/by/2.0/>.

Moreover, the colony occupies a relatively small sandy peninsula (Punta de la Banya, Ebro Delta, 2500 ha, Fig D.1.1.a-d) characterized by compacted sandy substrate with low and patchy halophyte vegetation which makes predator detection easy. We used number of carnivores detected annually by the Ebro Delta Natural Park Environmental Agency during systematic surveys as a proxy of predator abundance.

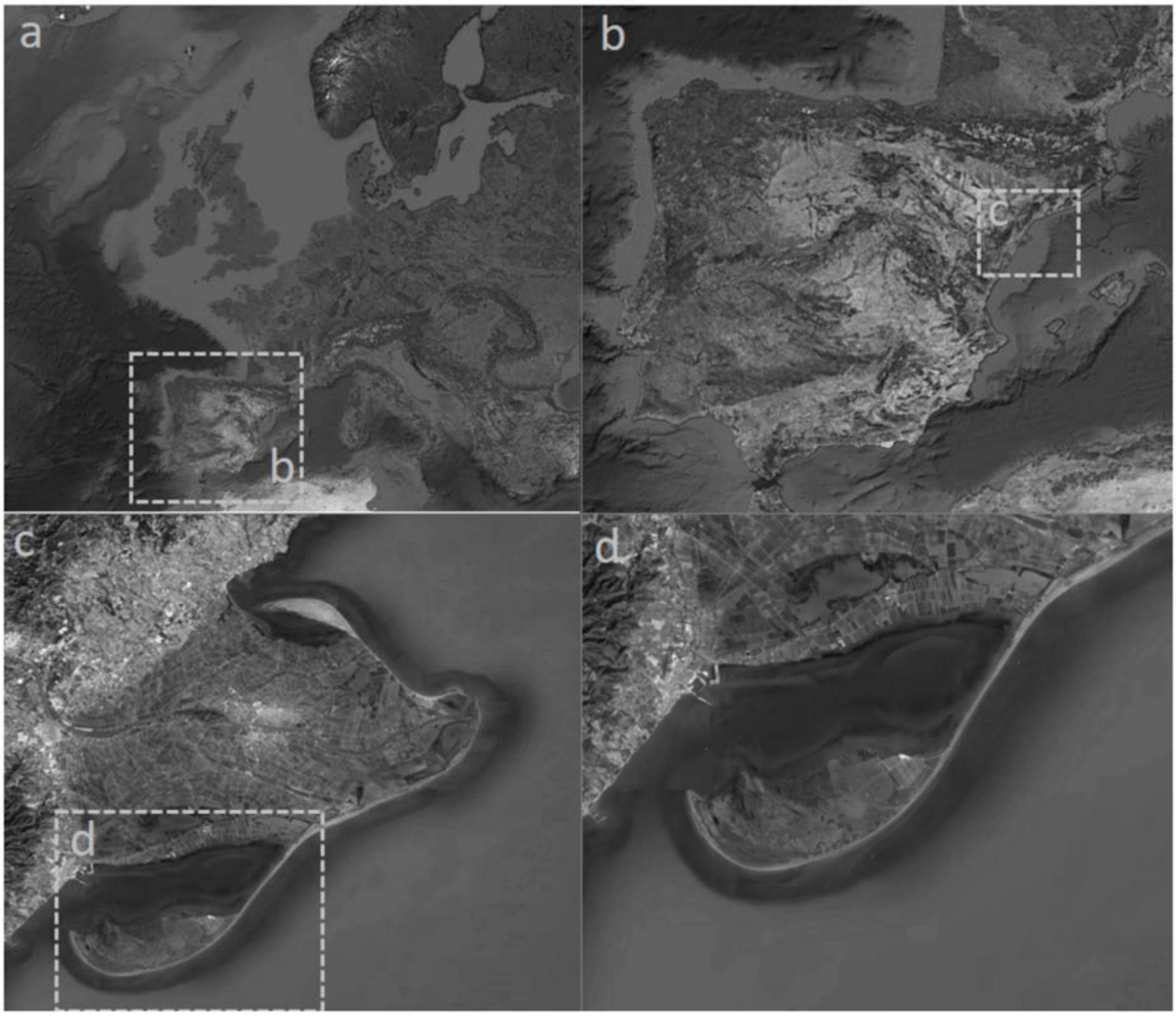

Fig. 17: Each panel zooms in the study area. Dashed line boxes represent the area zoomed in the next panel. a) Europe, b) Iberian Peninsula, c) Ebro Delta and d) Punta de la Banya. Maps copyright: Google, 2017 DigitalGlobe.

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D.1.2 Breeding performance

Parameters related to eggs are an excellent proxy of breeding conditions(Oro,D., L X 1996)1. In the period 1992–2016 breeding performance was monitored annually. During these years, we recorded clutch size (the number of eggs laid) and measured length (L) and maximum width (W) egg with a digital calliper to the nearest mm (see Oro et al. (1996)). Regular visits (median seven visits for the laying and incubation period lasting 30 days) allowed us to obtain unbiased estimates for clutch size. Egg volume (in cm3) was calculated using the equation: $V = \beta L W^2$, in which β was a species-specific constant parameter ($\beta = 0.476$ for Audouin's gull (Payo-Payo et al. 2017, Harris 1964), L and W expressed in cm. Egg volume and clutch size are often related to food availability (Payo-Payo et al. 2017, Oro et al. 1996). To account reduce the biases of food availability effects on egg volume we considered only egg volume of clutches with the mode clutch size by year. Moreover, we tested for potential correlations between predators intensity and food availability (tonnes of trawlers landed in the nearest fishing port) and they were independent of each other. Breeding success was estimated using the Lincoln-Petersen estimator (Williams et al. 2001, Oro and Ruxton 2001, Seber 2002). This estimator is based in the assumption that if a proportion of the population was marked in a first occasion, after complete mixing, a second sample was taken, then the proportion of marked chicks in the second sample would be the same as was marked initially in the total population. $N = MT/R$, N is population size, M is the number of chicks marked in the first occasion, R is the number of marked recaptured, T is the total number of chicks captured in the second occasion.

D.2 Extended results

D.2.1 Model selection and model parameter tables

Table 20: DF, degrees of freedom; DEV, deviance; AIC, Akaike's information criterion; ΔAIC, AIC difference with the best model; T, time; D, distance to the easternmost point of the breeding colony ; CS, clutch size; EGG VOL, egg volume; N_{ext}, number of patch extinctions; N_{col}, number of patch colonizations; N, number of occupied patches.

Model	DF	DEV	AIC	ΔAIC	P-value
D NO EFFECT	1	45.24	87	38.00	
D T	2	8.66	49	0.00	***
N$_{ext_{NOEFFECT}}$	20		148.07	0.00	
N$_{ext}PRESENCE$	19	0.00	150.07	2.00	
N$_{ext}ABUNDANCE$	19	0.24	149.83	1.76	
N$_{col}NOEFFECT$	21		131.90	0.00	
N$_{col}PRESENCE$	20	1.03	132.87	0.97	
N$_{col}ABUNDANCE$	20	-0.16	133.03	1.13	
N NO EFFECT	22		240.92	65.03	
N PRESENCE	21	67.03	175.89	0.00	***
N ABUNDANCE	21	-8.49	184.38	8.49	
EGG VOL NO EFFECT	4	257694	259759	41.00	
EGG VOL PRESENCE	5	257651	258377	0.00	***
EGG VOL ABUNDANCE	5	257681	259271	30.00	
CS NO EFFECT	23		-18.77	2.01	
CS PRESENCE	22	-0.07	-17.29	2.49	
CS ABUNDANCE	22	-0.08	-20.78	0.00	***

Table 21: Intercept (i) and slopes (β) for the fixed: predators' presence (β_{after}), predators' number (β_{Npred}), year (β_{year}) and random: nest and year ($\beta_{residual}$) effects on clutch size(CS), egg volume (EGG VOL), distance(D), number of occupied patches(N) Est, estimate; SE, standard error; Var, variance; SD, standard deviation. Models are noted as in Table 20.

	D		N		CS		EGG VOL	
Fixed	Est	SE	Est	SE	Est	SE	Est	SE
i	360.99	37.07	2.99	0.09	-9.89	2.68	63.67	0.59
β_{after}			0.75	0.09			-6.9	0.63
β_{Npred}					1.98	0.61		
β_{year}	-0.17	0.02						
Random							VAR	SD
i_{nest}							8.35	2.89
i_{year}							0.93	0.97
$\beta_{residual}$							13.64	3.69

D.2.2 Video

Video 1: Temporal evolution (1992-2015) of Audouin's gull breeding patches at Ebro Delta breeding colony. Circle size is proportional to the number of pairs breeding. Maps were built in R-Software (Team 2013). Video is available via <https://drive.google.com/open?id=0BzfbihtntuT0bXZUc09aeHpKNWc>.

D.2.3 Figures

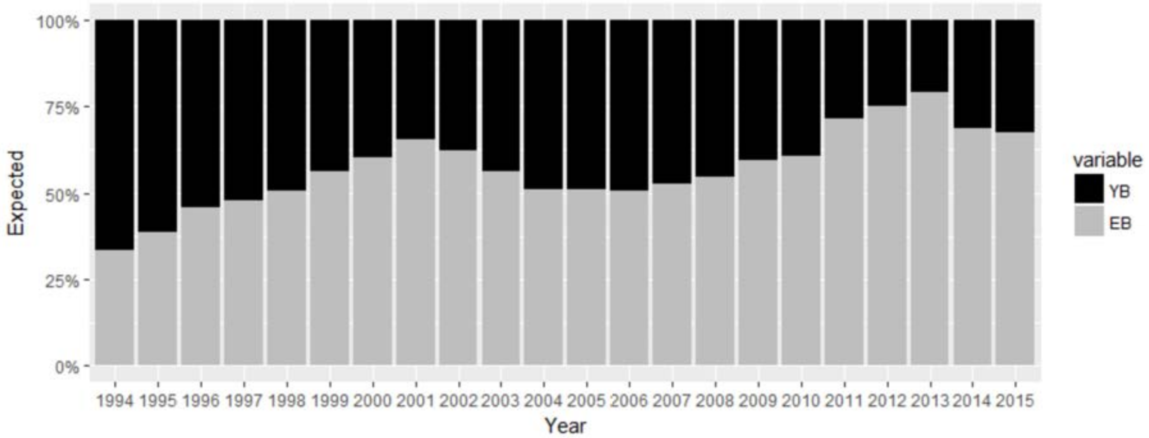

Fig. 18: Annual proportions of expected young and inexperienced breeders (YB) in relation to the expected experienced breeders (EB) at Ebro Delta Colony between 1994 and 2015.

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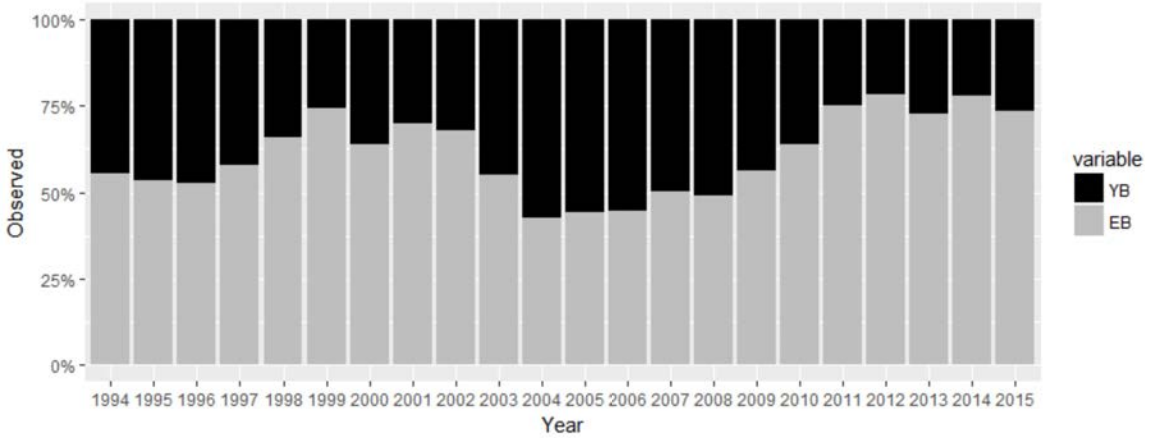

Fig. 19: Annual proportions of observed young and inexperienced breeders (YB) in relation to the expected experienced breeders (EB) at Ebro Delta Colony between 1994 and 2015.

VI | Articles

Ecological Applications, 25(8), 2015, pp. 2228–2239

Population control of an overabundant species achieved through consecutive anthropogenic perturbations

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Abstract. The control of overabundant vertebrates is often problematic. Much work has focused on population-level responses and overabundance due to anthropogenic subsidies. However, far less work has been directed at investigating responses following the removal of subsidies. We investigate the consequences of two consecutive perturbations, the closure of a landfill and an inadvertent poisoning event, on the trophic ecology ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$), survival, and population size of an overabundant generalist seabird species, the Yellow-legged Gull (*Larus michahellis*). We expected that the landfill closure would cause a strong dietary shift and the inadvertent poisoning a decrease in gull population size. As a long-lived species, we also anticipated adult survival to be buffered against the decrease in food availability but not against the inadvertent poisoning event. Stable isotope analysis confirmed the dietary shift towards marine resources after the disappearance of the landfill. Although the survival model was inconclusive, it did suggest that the perturbations had a negative effect on survival, which was followed by a recovery back to average values. Food limitation likely triggered dispersal to other populations, while poisoning may have increased mortality; these two processes were likely responsible for the large fall in population size that occurred after the two consecutive perturbations. Life-history theory suggests that perturbations may encourage species to halt existing breeding investment in order to ensure future survival. However, under strong perturbation pulses the resilience threshold might be surpassed and changes in population density can arise. Consecutive perturbations may effectively manage overabundant species.

Key words: adult survival; anthropogenic perturbation; Dragonera Island, Spain; food availability; Larus michahellis; *pest; population size; predictable anthropogenic food subsidies; seabird; stable isotope analysis; Yellow-legged Gull.*

INTRODUCTION

Human alterations of natural systems have triggered profound changes in ecosystem functioning and species communities (Vitousek et al. 1997). For instance, predictable anthropogenic food subsidies, such as landfill organic waste, have caused ecological and evolutionary changes at individual, population, community, and ecosystem levels (Oro et al. 2013 and references therein). Exploitation of subsidies alters not only dietary preferences but may increase body mass, body size, breeding performance, or survival on a wide range of species (Newsome et al. 2015). Subsidies are considered responsible for much of the demographic explosion of a wide range of so-called overabundant species, such as foxes, gulls, and rats (Duhem et al. 2008, Bino et al. 2010, Aplin et al. 2011). A large number of studies have tackled mitigation and management measures, such as direct culling aimed at reducing the ecological and social consequences of overabundant species (Bosch et al. 2000, Baker and Harris 2006, Merrill et al. 2006, Beasley et al. 2013). However, although these measures have been implemented worldwide, they have often turned out to be expensive and/or ineffective (Baker and Harris 2006, Oro and Martínez-Abraín 2007, Warburton and Norton 2009). The main flaw is that management measures often aim to mitigate the consequences of the human alteration rather than avert the occurrence of the alteration itself. However, recent European Union (EU) environmental policies are beginning to target the causes rather than their symptoms. For example, the final modifications to the Landfill Waste Council Directive (LWCD; European Commission 2008, EU 2009) aim to put an end to open-air landfill sites. In addition, these policies target a progressive reduction of predictable subsidies and are expected to trigger population control in some overabundant species. The exhaustive monitoring of the ecological processes ensuing after the closure of open-air landfill sites provides a unique perspective and understanding of the consequences to ecosystems of a forced reduction in supplementary feeding (Steigerwald et al.

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2015). Since seabirds are easily monitored and sensitive to changes in food availability, they provide a particularly good model for understanding the complexity and the efficacy of recent policy changes aimed at controlling overabundant species. For instance, changes caused by food limitation have been previously documented for seabird clutch size, egg volume, body size, breeding success, fecundity, adult survival, local recruitment, dispersal, and population size (Pons and Migot 1995, Harris et al. 1997, Oro and Pradel 2000, Oro and Furness 2002, Duhem et al. 2008).

Predictable food subsidies, together with the protection of suitable breeding areas in recent years, has led to an increase in large opportunistic gull populations (Duhem et al. 2008). Their growth has caused social annoyance as well as concerns for public health (Hatch 1996) and has trigged population control measures worldwide (Thomas 1972, Vidal et al. 1998, Bosch et al. 2000, Brooks and Lebreton 2001). For instance, Yellow-legged Gulls, *Larus michahellis* (YLG hereafter) in the Mediterranean basin have been subject to numerous culling programs aimed at controlling their numbers (the symptom) by targeting either a reduction in adult survival rates or breeding performance (Vidal et al. 1998, Brooks and Lebreton 2001, Duhem et al. 2008). Because seabirds are long-lived species, the reduction of adult survival is expected to have important population consequences (Sæther et al. 1996). However, direct culling had little effect on gull numbers because processes such as earlier recruitment or density-dependent higher fertility and immigration (Brooks and Lebreton 2001) were likely enhanced by high food availability, which might have boosted gulls' resilience to this type of perturbation (Oro and Martínez-Abraín 2007). Although food limitation has some impact on breeding performance, it is not expected to be particularly useful in controlling long-lived species; nevertheless, a long-term limitation of resources might be the key to controlling overabundant species by reducing recruitment (Oro and Martínez-Abraín 2007). When the two types of measures (food limitation and culling) are used together, their synergic or cumulative effects may lead to an important reduction in population size, although very little is known about the potential effects of linked management actions.

YLGs are large, colonial, and opportunistic seabirds distributed over the whole Mediterranean basin. YLG are known to exploit landfills to varying extents throughout their distribution range (Witt et al. 1981, Motis 1989, Bosch et al. 1994, Verdú del Campo et al. 1995, Ramos et al. 2009). Particularly, Ramos et al. (2011) assessed the importance of landfills on YLG in the western Mediterranean basin and demonstrated that landfill waste represents up to 60% of the diet of breeding YLG in our study colony. The recent explosion in YLG numbers has raised conservation concerns and several culling programs have been carried out in different locations. Despite these control measures, it is still the most abundant seabird in the Mediterranean (Zotier et al. 1999, Oro and Martínez-Abraín 2007).

We assessed the consequences on the ecology of YLG of two anthropogenic perturbations: (1) the closure of an open-air landfill site due to European Directives (EU 2009), which was estimated to represent half of its diet in terms of assimilated biomass (Ramos et al. 2011) and (2) the use of poison pellets in the study area to eradicate invasive pest, which caused indirect mortality in YLGs from primary (ingestion of pellets) and secondary (ingestion of poisoned rodents) poisoning (Mayol et al. 2012*a*). We investigated the changes in trophic ecology (dietary shift) and demographic parameters (population size and survival) of breeding YLGs that were attributable to the two consecutive anthropogenic perturbations. Life-history theory predicts that under limited food access, long-lived organisms will forego reproduction to avoid negatively affecting their future survival (Pugesek and Diem 1990, Oro et al. 1999). Thus, we expected that food limitation would trigger a dietary shift and differential resource exploitation, affecting breeding performance (Oro et al. 1995, Steigerwald et al. 2015) but not individual survival probability. Moreover, we expected that the inadvertent poisoning event would cause an increase in mortality rate due to the accidental poisoning of individuals. We expect that the combined effects of one action affecting reproductive performance and another affecting adult survival might trigger a decrease in population size. In addition, we expected our results to shed more light on the effects of consecutive perturbations and to provide a more comprehensive framework for superabundant species management.

METHODS

Study area and perturbations

Data were collected at Dragonera Natural Reserve, a 300-ha island off the coast of Mallorca (Balearic archipelago, Spain, 39°35′02″ N, 02°19′17″ E). This protected site hosts the largest-known YLG breeding colony in the archipelago (McMinn 2010). YLG nests can be found all over the island, with areas of gentle slope and low vegetation having higher density. The tourism industry on Mallorca ($\sim 10^7$ tourists/year, with a population of $\sim 10^6$ residents) has increased waste production and its availability at a single landfill site for opportunistic feeders. This anthropogenic subsidy was responsible for the doubling of the YLG Balearic archipelago population between 1983 (~7500 pairs) and 2000 (~14 000 pairs; McMinn 2010). Local managers estimated the number of gulls foraging at the landfill (~32 km from Dragonera) to range between 7300 and 15 500 depending on the season and the year (TIRME 2003). Following European Directives (EU 2009), the open-air landfill was transformed into an incineration plant in winter 2009–2010. This transformation made waste virtually inaccessible to gulls. In mid-winter of the year after the transformation (January and February

2011), an eradication campaign targeting the human-introduced rats (*Rattus rattus*), mice (*Mus musculus*), and rabbits (*Oryctolagus cuniculus*) was carried out on Dragonera (Mayol et al. 2012*b*). This campaign involved the aerial application of Brodifacoum, a second generation anticoagulant whose main mechanism is blocking epoxy-reductose enzyme activity. Without generating bait shyness, this leads to lack of blood clotting factors, followed by hemorrhages, and eventually death (Hadler and Buckle 1992). In the weeks following the spread of the poison, ~800 YLG carcasses were found on the island (Servei de Protecció d'especies et al. 2011). This can be considered a minimum estimate given that the search was not exhaustive and the areas with dense vegetation and surrounding waters were not surveyed (Servei de Protecció d'especies et al. 2011).

Trophic level and dietary shift

Nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and sulphur ($\delta^{34}S$) isotopic ratios can be used in ecological studies to evaluate dietary shifts (Ramos et al. 2011), since analyses of individual feathers provide unique isotopic information for very specific spatiotemporal periods (Hobson 2008). We evaluated the nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and sulphur ($\delta^{34}S$) isotopic ratios of the first primary feather (P1) on 68 unique breeding YLG individuals captured (see *Methods: Local survival analysis and estimates of population abundance*) in 2004 ($N = 12$), 2008 ($N = 18$), 2011 ($N = 18$), and 2013 ($N = 20$; Table 2). P1 feathers were collected during the incubation period (April–May). Feathers were removed by cutting the feather quill, which causes no damage to the individuals. The P1 feather is replaced by molt at breeding sites, and its isotopic value is an indicator of the diet of the previous breeding season. Laboratory procedures for preparing and processing feather samples were carried out following Ramos et al. (2011). Feathers were washed in a 0.25 mol/L sodium hydroxide solution, rinsed thoroughly in distilled water to remove any surface contaminants, dried in an oven at 60°C to constant mass, and ground to a fine powder in a freezer mill (Spex Certiprep 6750; Spex Industries, Metuchen, New Jersey, USA) operating at liquid nitrogen temperature. Subsamples of powdered material were weighed to the nearest microgram, placed in tin capsules, and crimped for combustion for C, N, and S isotope determination. Isotopic analyses were carried out at the Serveis Científico-Tècnics of the University of Barcelona (Spain) by means of a Thermo-Finnigan Flash 1112 (for N and C) and 1108 (for S; CE Elantech, Lakewood, New Jersey, USA) elemental analyzer coupled to a Delta-C isotope-ratio mass spectrometer via a CONFLOIII interface (Thermo Finnigan MAT, Bremen, Germany), and applying IAEA standards (IAEA CH6, IAEA CH7, and USGS 24 for C; IAEA N1, IAEA N2, and IAEA NO3 for N; and IAEA-S1, IAEA-S2, and IAEA-S3 for S) every 12 samples to calibrate the system and compensate for any drift over time. Samples from 2004 were analyzed separately from 2008, 2011, and 2013 but the same instruments and standards were used. Precision and accuracy was $\leq 0.1‰$ for $\delta^{13}C$ measurements, $\leq 0.3‰$ for $\delta^{15}N$, and $\leq 0.3‰$ for $\delta^{34}S$.

Results were expressed in delta (δ) notation (Bond and Hobson 2012). We used linear mixed models (LMM) to evaluate the effects of landfill closure, sex, and their interaction (Crawley 2007), with the year as the random effect (Zuur et al. 2009), to account for the effect of environmental variability on isotopic signatures. In addition, we estimated diet composition before and after landfill closure for males and females by applying Bayesian three-isotope ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values), three-endpoint (marine, crops and terrestrial environments, and refuse sites) mixing models to the isotopic values (SIAR, stable isotope analysis in R; Parnell et al. 2008). Ramos et al. (2011) recently evaluated the spatiotemporal variations the feeding ecology of YLG on the western Mediterranean region. Prey isotopic signatures were homogeneous among most of the localities studied, hence we included mean isotopic values ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) calculated in their study for the main food resources exploited by YLG in Dragonera (values from Table 5 in Ramos et al. 2011). Moreover, we used the consumer-discrimination factors provided by these authors.

Local survival analysis and estimates of population abundance

Breeding adults were trapped during the incubation period using a tent spring trap (see Steigerwald et al. 2015). We chose to trap individuals in accessible nests along the main south path of the island (4.5 km long) to increase re-sighting probabilities in the following years. In total, we trapped 206 YLG, which were marked using a Darvic plastic band (ProTouch, Saskatoon, Saskatchewan, Canada) with a unique alphanumeric code for subsequent individual identification from a distance using spotting scopes. Marking, re-sighting of live birds, and recovery of dead animals (99 and 12 cases, respectively) in March/April in 2007–2013 were used to build individual encounter histories and analyzed using multistate capture–mark–recapture recovery (CMRR) models to estimate survival, recapture, and recovery probabilities (Brownie and Hines 1993, Lebreton et al. 1999). Since all recoveries came from the colony site, CMRR models cannot distinguish mortality from permanent emigration to unobservable areas of the island. As a consequence, our estimates refer to apparent survival (Lebreton et al. 1992). We assessed the goodness-of-fit test (GOF) for the general model assuming that all parameters vary over time (Jolly–Move model; Brownie and Hines 1993, Pradel et al. 2003) using the software U-CARE 2.2.2 (Choquet et al. 2005, 2009). The global GOF test revealed no evidence of transient animals, meaning that there was no difference in the probability of being later reencountered

TABLE 1. Results of the goodness-of-fit tests for the general capture–recapture–recovery multistate model for male and female Yellow-legged Gulls (*Larus michahellis*) on Dragonera Island, Spain.

Test	χ^2	df	P	$\hat{c}$
Males				
3G.SR	2.90	5	0.72	0.58
3G.SM	1.66	4	0.80	0.41
M. Itec	3.54	5	0.62	0.71
M. Ltec	0.37	3	0.95	0.12
Global 3G	4.55	9	0.87	0.51
Global M	3.91	8	0.87	0.49
Females				
3G.SR	16.02	5	0.01	3.20
3G.SM	4.18	4	0.38	1.05
M. Itec	3.16	5	0.68	0.63
M. Ltec	5.62	4	0.23	1.41
Global 3G	20.20	9	0.02	2.25
Global M	8.82	9	0.45	0.98

Notes: Test components are listed as in Pradel et al. (2003), where 3G tests for transients' presence and M. tests for trap dependence. 3G.SR and 3G.SM test for among-individual homogeneity in survival; M.Itec and M.Ltec test for homogeneity in recapture process. Statistics are χ^2, chi-square statistic; df, degrees of freedom; $\hat{c}$, inflation factor, i.e., χ^2/df.

between new and old individuals encountered at a given time, and that there were no trap-dependence effects (i.e., no difference in the probabilities of being reencountered in the different stages at $i + 1$ between the animals in the same state at occasion i whether or not encountered at this date). Thus, the general model adequately explained the data ($\chi^2 = 37.483$, df $= 35$, $P = 0.356$; Table 1). The GOF test for females indicated the presence of transients, but since the global GOF was not statistically significant we used a variance inflation factor, $\hat{c} = 1.07$, to account for the remaining heterogeneity (Choquet et al. 2005, 2009). We identified a set of biological hypotheses (Fig. 1) and began by testing effects on a single parameter at a time (Lebreton et al. 1992). We considered the effect of year, sex, landfill closure, and the pest eradication campaign on local survival probability (Fig. 1). The landfill closure and pest eradication campaign effects were tested either as punctual or persistent depending on the temporal extent (short vs. long term, respectively) of the effect in the considered hypothesis (Fig. 1). Furthermore, we used the number of days spent searching for marked animals as a predictor of recapture probability and the effort (number of searching days) invested in searching for corpses by the Dragonera Natural Reserve team as a predictor of the recovery rate. We began by simplifying the structure of the recovery rate (λ) from a general model (E_0), assuming all three parameters to be dependent on time and sex. We then modeled recapture (p) and finally the survival parameter (φ). Note that models' rank did not change when the model selection began with a different parameter (results not shown). Models were implemented using the program MARK 7.1 (White and Burnham 1999). Models were selected using the second order Akaike information criterion AIC_c value and, in addition, deviances were scaled using the over-dispersion dispersion parameter (QAIC_c; Burnham and Anderson 2002). We considered the model with lowest AIC_c or QAIC_c and those within two points of $\Delta\text{AIC}_\text{c}$ or $\Delta\text{QAIC}_\text{c}$ (the difference in AIC_c and QAIC_c values, respectively) to be equivalent, and we used these models to produce final model-averaged parameter estimates (mean ± SE; Burnham and Anderson 2002). In this way, we included the effects of parameters obtained from separate models and accounted for model selection uncertainty (Burnham and Anderson 1998).

Each year, we estimated nest density in a 0.32-ha area (0.11% of Dragonera Island surface) with gentle slope and low vegetation as proxy of population size and for assessing its fluctuations over the study period. We assumed that despite that nest density might not be homogeneous within the island, the relative change in its value was a good indicator of population changes, as the surface occupied by the colony remained invariant. Five to nine observers walked the delimited area forming a transect line with a distance of ~3–5 m between each

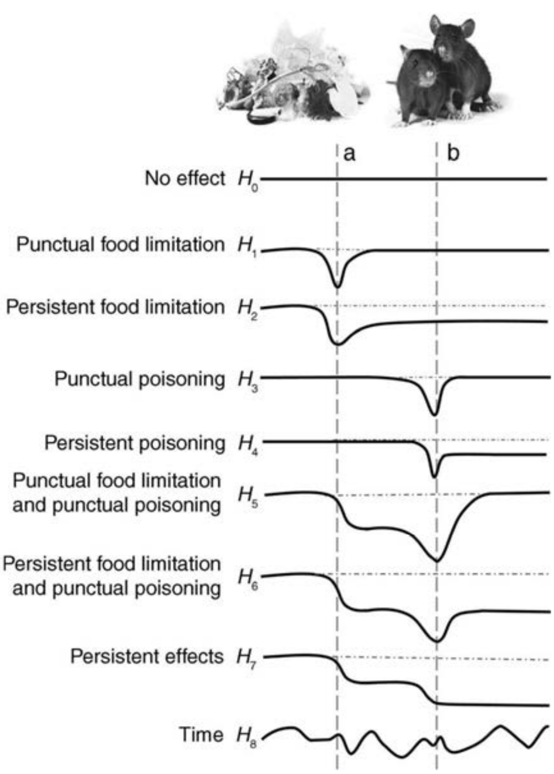

FIG. 1. Survival probability (Φ) shows qualitative representation under different biological hypotheses. Dashed lines a and b represent the landfill closure and the eradication campaign, respectively. Survival hypotheses are numbered in growing complexity and assigned to the analogous model on Table 1 (model number in parentheses): H_0 (M_0), H_1 (M_1), H_2 (M_2), H_3 (M_3), H_4 (M_4), H_5 (M_5), H_6 (M_6), H_7 (M_7), and H_8 (M_8).

TABLE 2. Values (mean ± SE) of nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and sulphur ($\delta^{34}S$) stable isotope signatures of male and female Yellow-legged Gulls at Dragonera Island before (2004 and 2008) and after (2011 and 2013) the landfill closure.

Variable, by sex	Before (‰)	After (‰)
Male		
$\delta^{15}N$	10.69 ± 0.12	11.11 ± 0.29
$\delta^{13}C$	−19.91 ± 0.10	−19.64 ± 0.27
$\delta^{34}S$	10.85 ± 0.62	13.95 ± 0.63
Female		
$\delta^{15}N$	10.50 ± 0.18	10.91 ± 0.22
$\delta^{13}C$	−20.13 ± 0.21	−19.94 ± 0.18
$\delta^{34}S$	11.48 ± 0.71	14.51 ± 0.60

other and marking all encountered nests. Observers shuffled position within the line and surveyed the transect a second time to recapture marked nests and count new ones. The number of nests in the area was then estimated by the Lincoln-Petersen estimator (Williams et al. 2001, Seber 2002). We used the delta method (Morgan 2000) to approximate the variance of the mean before and after the landfill closure and the pest eradication campaign. We then assessed if there was a population change after the events with a Z test (Zar 2010).

RESULTS

Trophic level and dietary shift

We analyzed nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and sulphur ($\delta^{34}S$) isotopic ratios before and after the landfill closure (Table 2). The model selection procedure showed no significant changes in $\delta^{13}C$ before and after the landfill closure (Table 3, model M_1; see Appendix: Table A1 for estimates). The landfill effect was not retained in the analysis of $\delta^{15}N$ (Table 3, M_1; Appendix: Table A1 for estimates), although that effect was present in an equivalent model ($\Delta AIC_c = 0.36$ for model M_2, Table 3; Appendix: Table A1 for estimates). All retained models for $\delta^{34}S$ (Table 3, M_2, M_4, and M_5; see Appendix: Table A1 for estimates) included the landfill effect as important, giving larger $\delta^{34}S$ values after landfill closure. Males and females had the same isotopic signature, however a sex effect was accounted for in two of the best three models of $\delta^{34}S$ (Table 2, M_4 and M_5; see Appendix: Table A1 for estimates), indicating a small (not statistically significant) difference in male and female diet. Model results for isotopic contents (Table 3, Fig. 2), together with the estimated percentage of diet diversity indicated by the SIAR analysis (Fig. 3), revealed changes in resource use after the landfill closure: the marine content of the diet increased while refuse diet content decreased, as expected.

Local survival and population size

The model selection procedure resulted in five models having more than 10% of the $QAIC_c$ weight and occurring within 1 point of $QAIC_c$ value (Table 4), impairing conclusions on the statistical significance of each single effect. This uncertainty was probably due to the complexity of the model used to join two types of information (recoveries and recaptures) and the relatively small data set available. Nevertheless, model-averaging techniques took this uncertainty into account and delivered weighted estimates of the parameters of

TABLE 3. Table summarizing the model selection for isotope signatures of Yellow-legged Gulls breeding on Dragonera Island, Spain.

Isotope signature and model	Model notation	np	AIC_c	ΔAIC_c	w
$\delta^{13}C$					
M_1	**$\delta^{13}C$**	**1**	**170.40**	**0.00**	**0.58**
M_2	$\delta^{13}C_{LANDFILL}$	2	173.20	2.75	0.15
M_3	$\delta^{13}C_{SEX}$	2	172.60	2.19	0.20
M_4	$\delta^{13}C_{LANDFILL+SEX}$	3	175.10	4.65	0.06
M_5	$\delta^{13}C_{LANDFILL+SEX+LANDFILL\times SEX}$	4	177.50	7.01	0.02
$\delta^{15}N$					
M_1	**$\delta^{15}N$**	**1**	**187.40**	**0.00**	**0.43**
M_2	$\delta^{15}N_{LANDFILL}$	2	187.70	0.36	0.36
M_3	$\delta^{15}N_{SEX}$	2	190.40	2.98	0.10
M_4	$\delta^{15}N_{LANDFILL+SEX}$	3	190.50	3.11	0.09
M_5	$\delta^{15}N_{LANDFILL+SEX+LANDFILL\times SEX}$	4	192.60	5.27	0.03
$\delta^{34}S$					
M_2	**$\delta^{34}S_{LANDFILL}$**	**2**	**321.70**	**0.00**	**0.33**
M_4	$\delta^{34}S_{LANDFILL+SEX}$	3	322.00	0.35	0.28
M_5	$\delta^{34}S_{LANDFILL+SEX+LANDFILL\times SEX}$	4	322.10	0.39	0.28
M_1	$\delta^{34}S$	1	325.20	3.54	0.06
M_3	$\delta^{34}S_{SEX}$	2	325.40	3.69	0.05

Notes: The best model for each isotope is shown in bold. All models include year as random factor. Notations are LANDFILL, landfill closure effect; SEX, sex effect; +, additive effect; ×, interaction effect; np, number of parameters; AIC_c, corrected Akaike's information criterion; ΔAIC_c, AIC_c difference with the best model; w, Akaike weight.

interest according to the model $QAIC_c$ value. The model with the lowest $QAIC_c$ value (model M_0, Table 4) indicated a constant survival, i.e., independent of sex and the perturbations or the years considered. Averaged estimates were calculated for models M_{0-3} and M_5, which were within 2 $QAIC_c$ points of the one with the lowest value (M_0). All these models included the effect of food limitation and averaged estimates suggest that the closure of the landfill caused an 8% drop in survival (from 0.71 ± 0.07 in 2009 to 0.63 ± 0.07 in 2010). Similarly, the averaged estimates immediately after the pest eradication program indicated an additional 2% drop in apparent survival (from 0.63 ± 0.07 in 2010 to 0.61 ± 0.11 in 2011). The two synergic perturbations caused a 10% drop in survival probability when compared to the value before the landfill closure.

Nest survey data clearly showed a decrease in size of the nesting population after the two perturbations. The number of nests in the surveyed area first decreased by 37% after the landfill closure (from 92.13 ± 4.01 in 2009 to 58.05 ± 5.71 in 2010) and had an additional drop of 65.99% after the pest eradication campaign (from 58.05 ± 5.71 in 2010 to 20.19 ± 2.30 in 2010; Fig. 4). Both perturbations caused a statistically significant change in nesting population size ($Z = 13.78$, $P < 0.00001$ and $Z = 17.19$, $P < 0.00001$ for landfill closure and poisoning campaign, respectively). The two synergic perturbations caused a 78% drop in nesting population size when compared to the value before the landfill closure (Fig. 4).

We found no significant differences in either survival between males and females, or over time (Table 4, M_{8-13}). The search for carcasses and the sampling effort (Table 4, M_9 and M_{12}, respectively) well predicted recovery and recapture probabilities, respectively. Average recapture probabilities ranged between 0.24 (SE = 0.06) and 0.47 (SE = 0.07; Fig. 5b), while recovery probabilities were constant (0.07 ± 0.03), except for a 0.18 (SE = 0.09) increase in 2010 when a specific search for carcasses was conducted (Fig. 5c).

DISCUSSION

We assessed trophic and demographic changes in YLG after two consecutive anthropogenic perturbations, namely a food reduction after the closure of an open-air landfill and the accidental poisoning due to a campaign targeting the eradication of invasive mammals. Extensive research has been performed on the effects of predictable anthropogenic food sources across taxa (see reviews in Oro et al. 2013, Newsome et al. 2015). Specifically, several studies on gulls have assessed the effects of food availability on several parameters such as diet (Ramos et al. 2011), survival (Oro et al. 1999), and population size (Oro et al. 1999, 2004, Duhem et al. 2008). These studies recorded that a decrease in the availability of food subsidies caused changes in resource exploitation and increased dispersal, whereas survival remained constant. However, none of these studies analyzed all these parameters simultaneously, nor did they evaluate the consequences of the combined effect of food limitation and additive mortality on population dynamics.

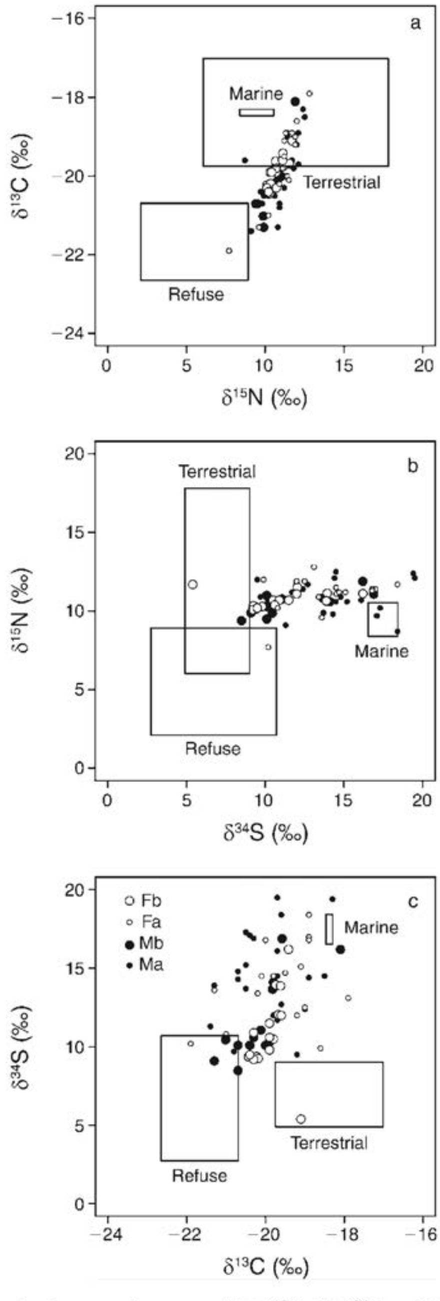

FIG. 2. Isotope signatures of (a) $\delta^{13}C$, (b) $\delta^{34}S$, and (c) $\delta^{15}N$ of male (solid circles) and female (open circles) Yellow-legged Gulls (*Larus michahellis*) breeding on Dragonera Island, Spain, before (large circles) and after (small circles) the landfill closure. Tissue from first primary feathers. Rectangles represent mean ± 1.96 SE isotopic signature from marine, crops and terrestrial, and waste food sources, as calculated by Ramos et al. (2011).

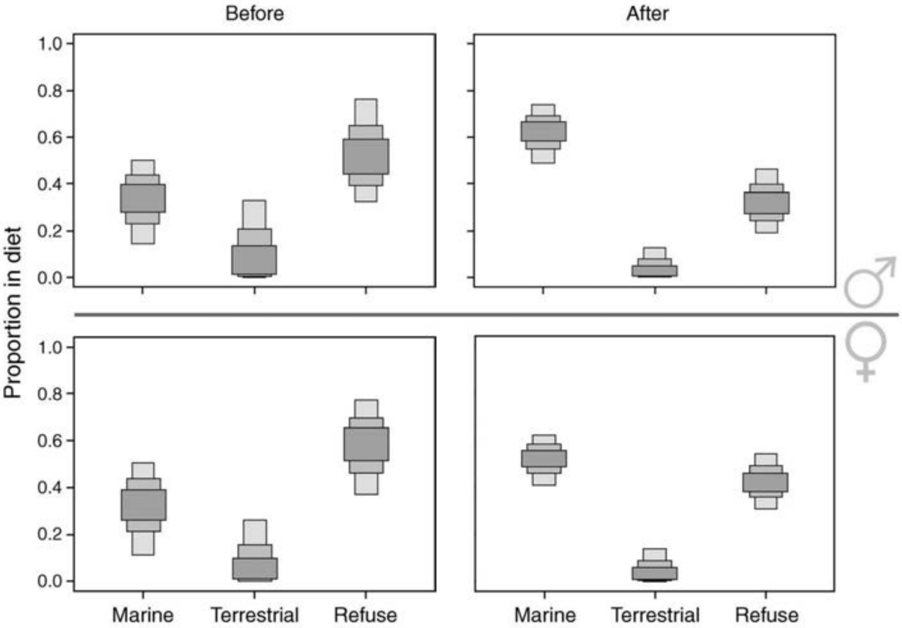

FIG. 3. Diet estimates of marine, terrestrial, and waste resources (true proportions and their Bayesian credibility intervals including 50%, 75%, and 95% of the posterior distributions) estimated by stable isotope analysis in R mixing modeling based on C, N, and S isotopic signatures from the first primary (P1) feathers of Yellow-legged Gulls from Dragonera Island (left) before and (right) after landfill closure in males (upper panels) and females (lower panels). Sample sizes are $N = 23$ males before landfill closure, $N = 9$ males after closure, $N = 25$ females before, and $N = 15$ females after.

Predictable anthropogenic food can be a low-quality resource (the so-called junk-food; see Pierotti and Annett 1991, Annett and Pierotti 1999, Grémillet et al. 2008, Genovart et al. 2010), but gulls appear to adjust their diet in accordance with the availability, rather than with the quality, of foraging resources except when feeding chicks (Pons 1992, Pedrocchi et al. 1996, Oro et al. 2004). During the last few decades, landfills have provided YLG with a vast food surplus, leading to higher carrying capacity and rapid population growth (Duhem et al. 2008). It is likely that when access to this food was restrained, gulls were forced to exploit more energetically demanding and less predictable (unless obtained from fishery discards) marine prey (Bartumeus et al. 2010). We present partial evidence of this dietary shift toward marine resources in YLG trophic behavior

TABLE 4. Modelling of survival (Φ), recapture (P), and recovery (λ) probabilities of Yellow-legged Gulls on Dragonera Island, Spain.

Model	Model notation	np	$QAIC_c$	$\Delta QAIC_c$	*w*
$\mathbf{M_0}$	$\mathbf{\Phi.\ P_E\ \lambda_B}$	**5**	**579.26**	**0.00**	**0.23**
M_1	$\Phi_{LANDFILL}!\ P_E\ \lambda_B$	6	579.76	0.50	0.18
M_3	$\Phi_{PEST!}\ P_E\ \lambda_B$	6	580.17	0.91	0.15
M_2	$\Phi_{LANDFILL\infty}\ P_E\ \lambda_B$	6	580.18	0.92	0.15
M_5	$\Phi_{LANDFILL!+PEST!}\ P_E\ \lambda_B$	7	580.21	0.95	0.14
M_6	$\Phi_{LANDFILL\infty+PEST}!\ P_E\ \lambda_B$	7	581.82	2.56	0.06
M_7	$\Phi_{\ LANDFILL\infty+PEST\infty}\ P_E\ \lambda_B$	8	582.34	3.08	0.05
M_4	$\Phi_{PEST\infty}\ P_E\ \lambda_B$	6	584.38	5.11	0.02
M_8	$\Phi_T\ P_E\ \lambda_B$	10	584.88	5.62	0.01
M_9	$\Phi_{T+SEX}\ P_E\ \lambda_B$	15	592.48	13.21	0.00
M_{10}	$\Phi_{T+SEX}\ P_T\ \lambda_B$	20	595.99	16.73	0.00
M_{11}	$\Phi_{T+SEX}\ P_{T+SEX}\ \lambda_B$	26	608.36	29.10	0.00
M_{12}	$\Phi_{T+SEX}\ P_{T+SEX}\ \lambda_{B+SEX}$	28	612.4	33.14	0.00
M_{13}	$\Phi_{T+SEX}\ P_{T+SEX}\ \lambda_{T+SEX}$	32	617.66	38.40	0.00

Notes: The best model is shown in bold. Model subscripts refer to hypotheses in Fig. 1. Notations are LANDFILL, landfill effect; T, year effect; B, recovery effort; E, recapture effort; PEST, pest eradication effect; !, punctual; ∞, persistent; ·, no effect; +, additional effect; np, number of estimable parameters in the model; $QAIC_c$, Akaike's information criterion corrected for sample size, number of parameters, and over-dispersion; $\Delta QAIC_c$, $QAIC_c$ difference with the best model; *w*, weight of the model.

following a landfill closure. Since we were only interested in changes occurring at a population level, we did not account for the differences between individual's trophic behavior (Navarro et al. 2010). The evidence was clear in sulphur isotope signature: YLG exploited significantly more marine resources after the landfill closure; however, we failed to detect a change in carbon isotope signature. The threshold to detect a change in sulphur isotope signatures lies around 10‰ while it is 3‰ for carbon isotope signatures (see Fig. 2 and mean isotopic values in Ramos et al. 2011). We attribute our non-statistically significant difference in carbon isotope signatures to a lack of statistical power, and hence cannot ascertain nor deny a possible effect. However, other YLG colonies have been observed to follow the same pattern (see Arizaga et al. 2013). The use of $\delta^{34}S$ is commonly used to characterize the effect of marine food sources on various species (Lott et al. 2003, Natsumeda et al. 2015). Moreover, Moreno et al. (2010) demonstrated the potential of using $\delta^{34}S$ alone to distinguish not only between terrestrial and marine prey, but also between different marine prey species. Pedro et al. (2013) showed that exploitation of waste food by large, opportunistic gulls is a relatively new strategy that appeared less than 100 years ago. It is therefore not surprising that YLG from Dragonera were able to increase their consumption of marine and other terrestrial prey after food from landfill waste became unavailable. Moreover, other studies have also demonstrated a reduction in YLG waste consumption in this study area after the landfill closure (Ramos et al. 2011). It therefore seems reasonable to conclude that a diet change towards a marine diet occurred as a result of the landfill closure.

Low food availability is also known to increase intraspecific competition and reduce the contribution of each individual to the next generation (Begon et al. 1996). Breeding seabirds suffering from food limitation face survival vs. reproduction trade-offs, and they are expected to forego current reproduction to guarantee adult survival prospects in order to increase the odds of future generations living under favorable conditions (Pons 1992, Pons and Migot 1995, Oro 1999, Sanz-Aguilar et al. 2008). Previous studies on gulls found severe impacts on breeding performance under different levels of food availability (Pons 1992, Pons and Migot 1995, Oro 1996). Particularly, our colony suffered a significant decrease in breeding performance (clutch size and egg volume) after landfill closure (Steigerwald et al. 2015). Moreover, Steigerwald et al. (2015) suggested that a dietary switch, which we confirmed, might not have been sufficient to fully cover the energy requirements of the local population. Foregoing reproduction to guarantee adult survival acts as a buffer mechanism against environmental variability and allows animals to cope with moderate environmental perturbations. Nevertheless, when food is in very short supply it can even affect body mass and local adult survival in long-lived seabirds (Oro and Furness 2002). This appears to be the case for our population, given the recorded drop in YLG body condition (Steigerwald et al. 2015) along with a slight decrease in local survival rates after landfill closure. Gulls usually form spatially structured populations (Oro et al. 2003) and given that previous studies have shown that dispersal occurs following environmental perturbations (Oro et al. 2004, Fernández-Chacón et al. 2013), we suggest that food limitation has triggered not only mortality but also permanent emigration (through breeding dispersal) to neighboring populations (Bosch 2000, Oro 2003).

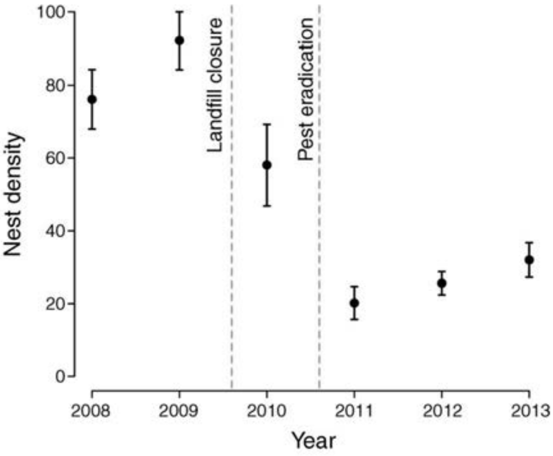

FIG. 4. Changes in nest density as a proxy of population size (mean ± 1.96 SE) of Yellow-legged Gulls breeding on Dragonera Island, Spain. Dashed lines indicate landfill closure and pest eradication campaign dates.

These findings agree with previous work on other seabird species (Oro 1999, Oro et al. 2004, Duhem et al. 2008), which found a close correlation between anthropogenic food availability and colony size. Our work suggests that the decrease in food availability caused a dietary shift towards marine resources. The dietary shift was followed by a partial reduction in breeding performance (Steigerwald et al. 2015), leading to an increase in mortality and dispersal. Finally, the cumulative effects of poisoning magnified an already severe decrease in population size through real adult mortality. Despite that many individuals might have died or emigrated from the study area, those remaining exhibited similar survival compared to pre-perturbation values. Another possible explanation for why population size and survival follow different response patterns after these perturbations is that poisoning was intended to cause nonselective mortality across the whole population, thus also affecting non-breeders and immature gulls, but our survival estimates came only from breeding adults. Alternatively, the termination of the waste food surplus might have decreased the carrying capacity of the system and the population size could therefore have declined to match this new population

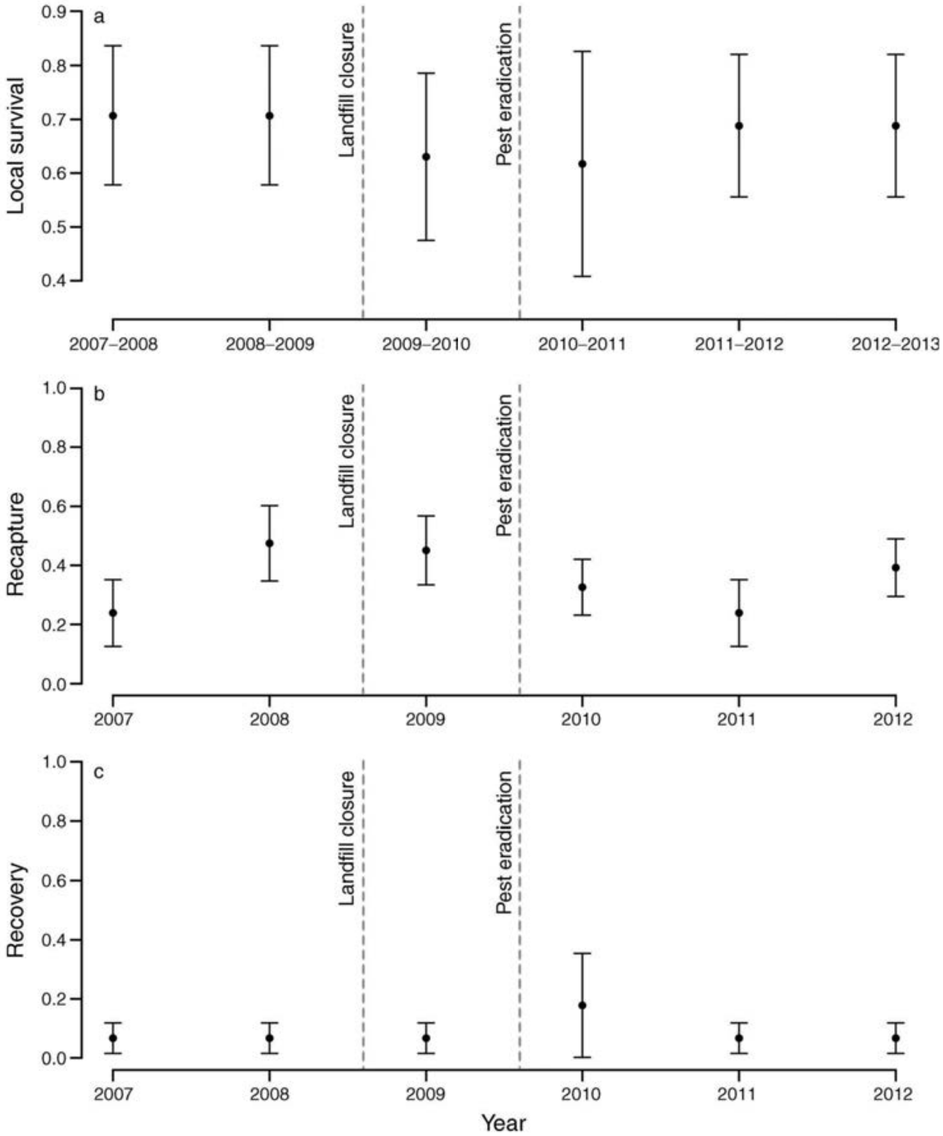

FIG. 5. Temporal variability in the estimated probabilities (mean and 95% CI) of (a) local survival, (b) recapture, and (c) recovery (95% CI) of Yellow-legged Gulls on Dragonera Island in 2007–2013 as estimated by the model-averaging of the five best equivalent models with $\Delta QAIC_c < 2$ ($QAIC_c$, Akaike's information criterion corrected for sample size, number of parameters, and over-dispersion; $\Delta QAIC_c$, $QAIC_c$ difference from the best model).

ceiling, while also influenced by the additive mortality from poisoning. We predict that population size will slowly increase in the coming years until it stabilizes at a new demographic equilibrium, however it will not reach the levels recorded before the two perturbations (Bosch et al. 2000).

Implications for the management of overabundant species

The food limitation and the mammal eradication campaign through poisoning were not specifically intended for the management of YLG populations. However, these actions allowed us to explore the implications of the combined effect in controlling of consecutive actions on the management of a so-called overabundant species. Many populations of overabundant species of birds and mammals are subject to extensive management programs designed to control their numbers (Mate et al. 1998, Anderson and Devlin 1999, Twigg and Kent Williams 1999, Bosch et al. 2000). These actions mainly aim to either reduce breeding success (Thomas 1972, Merrill et al. 2006) or to eliminate adults by culling (Bosch et al. 2000, Baker and Harris 2006). Such management is expensive and ineffective in the long term if applied in isolation (Baker and Harris 2006, Merrill et al. 2006, Oro and Martínez-Abraín 2007). We present evidence of how these two consecutively occurring perturbations have been extremely effective in reducing the population density of a generalist opportunistic bird, which has not recovered in the three years following these events. Under strong perturbation pulses (Martínez-Abraín et al. 2012) or intense environmental variability (Harding et al. 2011), the density-dependent responses of demographic parameters appear insufficient to buffer population changes. Although an isolated perturbation, such as poisoning, seemed to have an important short-term effect, it is reasonable to believe that it was the closure of the landfill site that led to a permanent decrease in the carrying capacity of the system and hence a long-lasting reduction in population numbers, as previously suggested by Oro and Martínez-Abraín (2007). Cumulative effects of consecutive perturbations are likely to become a useful tool in the control of overabundant populations. Nevertheless, despite the potential that these results have for the implementation of more effective management actions of overabundant species, caution must be taken because their long-term consequences are still unknown.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-2090.1.sm

Data Availability

Data associated with this paper have been deposited in CEDAI (Centro de Datos Imedea):

M-ARRAY_Larus michahellis_Dragonera_2007_2013: http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=c867ca26-7b03-4dcb-ac26-7ef0ab536762

Stable Isotope Signature (CNS)_ Larus michahellis_Dragonera 2004_2008_2011_2013: http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=280c2ad4-5204-4dde-b703-2ece5625730f

Nest abundance_Larus michahellis_Dragonera_2008_2013: http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=be15329b-5f71-4b9c-bd02-5cddcb67a553

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Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird

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Conditions during early life, including maternal cohort effects, can influence the future fitness of individuals. This may be particularly true for long-distance migrating birds, because, apart from conditions experienced by cohorts during rearing, conditions during early life in regions far from breeding grounds may also influence their population dynamics. Very little is known about the fitness consequences of those conditions experienced by juveniles after independence, especially in wild populations and for long-lived birds. We used multi-event capture–recapture–recovery models and a unique 26-year dataset for the Audouin's gull (*Larus audouinii*) to assess for the first time whether survival was influenced by early conditions, both during the rearing period (i.e. a maternal cohort effect potentially affected by density dependence) and the first winter (i.e. a cohort effect driven by climate when birds disperse to wintering grounds). Our results show that juvenile survival was highly sensitive to early-life conditions and that survival decreased with stronger density dependence and harsh climate. The two consecutive cohort effects were of similar magnitude and they may represent a selection filter. Thus, early-life conditions had a strong impact on survival, and neglecting this complexity may hinder our understanding on how populations of long-lived animals fluctuate and respond to perturbations.

1. Introduction

Conditions during early life can determine an individual's future fitness [1]. Those conditions are known as cohort or silver-spoon effects, and have been widely explored on a large range of vital rates in many taxa (see electronic supplementary material S1) [2–5]. Individuals facing harsh early-life conditions are expected to experience higher fitness costs later in life [1]. Harsh conditions include unfavourable climate, high population size, low habitat quality, poor parental quality and low food availability, and their potential interaction (see electronic supplementary material S1) [2–5]. The ability of offspring to compensate for a poor start in life determines whether early-life conditions have short- or long-term fitness consequences [6–8]. The former, also known as numerical effects, involve changes in traits such as pre-breeding survival, birth weight, birth date and body growth; the latter, known as delayed quality effects, affect future breeding performance and thus result in changes in the age of first breeding attempts, lifetime reproductive success and adult survival [2–5,9–13]. Environmental forcing in early life drives complex trade-offs between vital rates, and thus many of the effects noted above are likely to be interrelated [10,14]. Overall, early-life conditions may generate differences in vital rates between cohorts and can have important demographic consequences. For instance, cohort differences may result in delays in a population's response to environmental conditions that could destabilize its population dynamics [1].

Comparatively, far more attention has been directed at explaining the effects of early-life conditions on reproduction rather than on survival [10,15]. Within survival studies, substantial research describes the effects of early-life conditions under controlled experimental conditions [3,16] but much less is known about

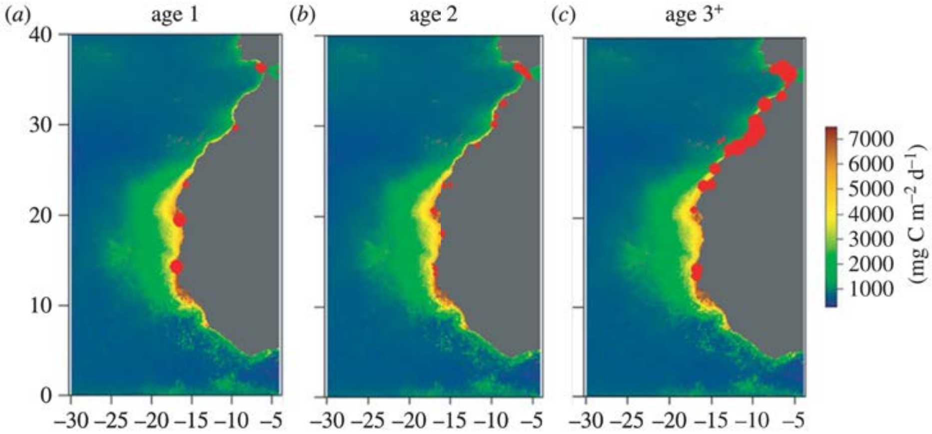

Figure 1. First winter conditions for Audouin's gulls, expressed as the average winter net primary production during 2002–2012 (mg C m^{-2} d^{-1}) on the north-west African coast, which influenced the availability of small pelagics. (*a*) First winter resightings of animals marked at the Ebro Delta (red dots) and (*b*,*c*) those resightings for older birds (red dots). The size of red dots is proportional to the number of individuals resighted. Resighting data were provided by the Catalan Ringing Office (www.ornitologia.org). (Online version in colour.)

wild populations of long-lived species [3,13,16]. Additionally, it is likely that the processes underlying the strong early-life selection pressures on survival, which lead to high and stable adult survival rates in long-lived species, are not limited to the rearing period [17]. For example, conditions experienced during winter may give rise to important changes in demographic rates such as recruitment, dispersal and even survival [18]. Nevertheless, winter conditions have been seldom considered as a type of cohort effect, even though these conditions may primarily affect juveniles. Thus, first winter conditions are likely to play a key role in the dynamics of natural populations, and their integration into early-life condition studies should therefore be considered. Yet, in some long-lived species, and particularly in birds, juvenile stages are often elusive and information about critical periods other than the breeding period is scarce [19].

Here, we explore the potential survival costs of a bad start in life in a long-lived bird, the Audouin's gull (*Larus audouinii*). We tested the survival costs associated with the conditions experienced by individuals during two critical early-life periods: the rearing phase and their first winter. Food is a key factor shaping population dynamics. Density dependence and climate, which regulate food availability, are likely to be crucial during these two life phases [20]. We predicted that individuals belonging to cohorts experiencing harsh environmental conditions during its first year (i.e. low food availability during both rearing and wintering periods) would endure greater survival costs later in life. In addition, we predicted that, since the study species is a long-lived bird, these effects would be strong in the first years of life and weak or non-existent on adult survival [7,19].

2. Material and methods

(a) Demographic data

We collected demographic data in Punta de la Banya (Ebro Delta, Spain; 40°37′ N, 00°35′ E), a flat sandy peninsula of roughly 2600 ha. The site holds around 60% of Audouin's gull's world population [21]. During 1988–2012 a total of 24 038 chicks were individually marked at fledging using a plastic band with a unique alphanumeric code. A total of 33 322 resightings and 552 recoveries were used in the analyses. Resightings were made during the breeding season (April–July) using spotting scopes. Recoveries of dead birds took place at the study site (authors' own fieldwork) and abroad (information provided by ringing offices).

(b) Environmental data

We tested whether survival was affected by conditions experienced during the rearing period and after independence, during the first winter along the northwestern African coast. As a proxy of rearing conditions we used food availability per capita [22,23]. Audouin's gull is a long-lived seabird that breeds colonially from April to July and usually lays three eggs. The species feeds mainly on small pelagics [24], and discards from trawling fleets can represent up to 75% of their diet during the breeding season [25]. In the study area, La Ràpita is the most important fishing harbour and accounts for 60% of the catch in number and 74% in total power. Thus, we took trawling landings at La Ràpita as a proxy of food availability in June, when chicks are under parental care. We then divided this proxy of food availability by population size of both Audouin's and yellow-legged gulls (*L. michahellis*), the most abundant sympatric species that exploits discards [25], to account for density dependence of the guild through interference competition and obtained the proxy of food availability per capita (hereafter DD). As a proxy of first winter conditions, we used the North Atlantic Oscillation climatic index during December–March (hereafter W_{NAO}), because gulls disperse during winter mostly to the Senegambia region [26]. This long-distance dispersal decreases with age, and most birds do not cross to Africa as they become older (figure 1) [26]. High positive W_{NAO} values are associated with the intensification of upwelling and thus with higher small pelagic fish availability [27]. DD and W_{NAO} index are independent of each other ($R^2 = 0.011$, $p = 0.636$).

(c) Modelling and hypothesis testing

Models were constructed in a multi-event capture–recapture framework, which addresses state uncertainty by relating the true state of the individual to the observed event via a series of conditional probabilities [28]. Goodness-of-fit test (GOF; see electronic supplementary material S2) suggested the presence of both trap-dependence and transience effects. After accounting for them, an acceptable variance inflation factor of 1.42 was obtained and used to correct all models constructed in E-SURGE [29,30]. Based on the GOF results we built models with four states

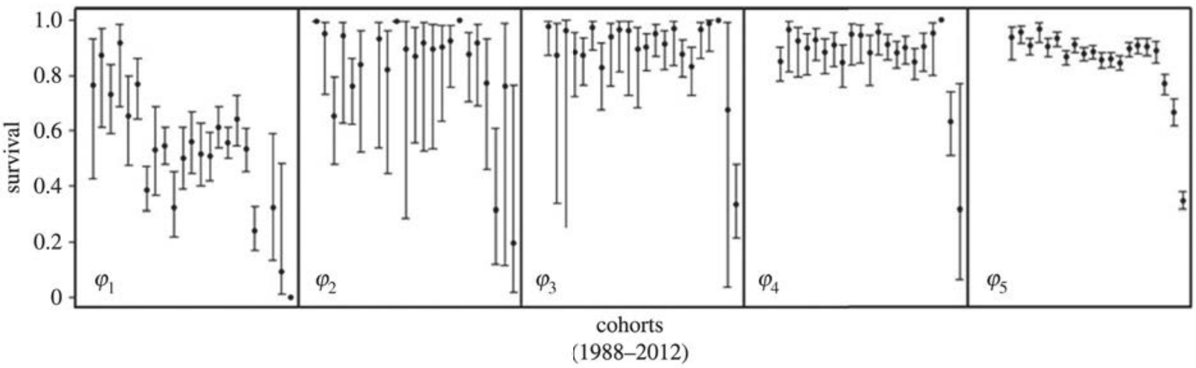

Figure 2. Annual survival (95% CI) of Audouin's gulls breeding in the Ebro Delta in 1988–2012 (each panel represents one of the five age classes retained by the best model; see electronic supplementary material S4.1).

(Aa, alive and trap-aware; Au, alive trap-unaware; Dr, recently dead; Dl, dead long ago) and three events (0, not seen; 1, seen alive; 2, seen dead; see electronic supplementary material S3). We used previous knowledge of the species [31–33] to design our initial exploratory set of models and select the best general model structure based on QAICc criterion (see the electronic supplementary material S4.1) [31–36]. We tested the absence of long-term cohort effects by running additive and interaction models including cohort and age effects. Once confirmed, we used the best general model to run different models, including the effect of DD and W_{NAO} in early life and their additive and interaction effects. Finally, we calculated the fraction of temporal variation explained by each covariate (DD and W_{NAO}) using ANODEV [32] (see electronic supplementary material S5). This was first tested in the general model with the best age structure and then in each of the young age classes in order to evaluate their temporal extent.

3. Results

The best recapture structure retained three age classes with different recapture probabilities, time and a trap awareness effect (STEP1; see electronic supplementary material S4.1). The model including temporal variation in recovery probabilities performed the best (STEP2; see electronic supplementary material S4.1) and the best structure for survival included five age classes with an interaction with year (STEP3; see electronic supplementary material S4.1 and S4.2 for model estimates; figure 2). We also evaluated the potential effects of early-life environmental covariates on survival. Models including DD and W_{NAO} covariates performed poorly in terms of QAICc compared with the best model, the time-varying model (see electronic supplementary material S4.3), but they explained large proportions of survival variability. DD explained 34% of survival variability, W_{NAO} explained 17% of survival variability, and the models including additive and interaction effects explained 42% and 50% of survival variability, respectively (see electronic supplementary material S4.3; all $p \leq 0.002$).

Once the effect of both DD and W_{NAO} had been confirmed, we evaluated their effects on each of the five ages considered. DD, and W_{NAO} had a strong influence on Audouin's gull survival but the effect faded after the first year of life (beta estimates and 95% confidence intervals for first-year survival φ_1: $\beta_{DD} = 0.625$ (0.248, 1.001), $\beta_{WNAO} = 0.464$ (0.376, 0.551); see electronic supplementary material S4.4 showing beta estimates for each model). Offspring born under high food availability per capita and those that experienced mild first winters (high W_{NAO} values) had increased first-year survival rates. DD and W_{NAO} explained similar amounts of survival variability — about 50% of first-year survival ($p = 0.000$; figure 3; electronic supplementary material S4.5). The model including both DD and W_{NAO} conditions explained a significant 62% of first-year survival ($F_{2,\ 19} = 15.52$, $p < 0.001$; electronic supplementary material S4.5). Models including an interaction effect do not explain any extra variance compared with the models including only the additive effect.

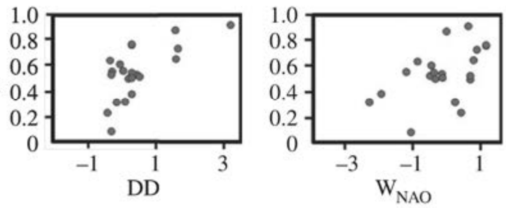

Figure 3. Relationship between first-year survival (φ1) of Audouin's gulls breeding in the Ebro Delta and tonnes of fish landed by trawlers *per capita*, including Audouin's and yellow-legged gulls (DD.); and W_{NAO}, Northern Atlantic Oscillation index, during the first winter of life.

4. Discussion

Several previous studies show that the effects of early-life conditions on fitness components can be important: the harsher the conditions an individual experiences during early life, the higher fitness costs the individual will undergo [1,3,4,6]. However, few studies have attempted to unravel the fitness consequences of early-life conditions in critical periods other than the rearing period, especially in wild populations [3]. We evaluate for the first time both the effects of early-life conditions experienced during rearing, but also during the first winter on the survival of a long-lived bird. Here, we find that both rearing and first winter conditions influenced first year survival. Although harsh early-life conditions can have consequences for long-term fitness, their influence is usually most pronounced during early-life stages [1,10]. We also show here that in Audouin's gulls, harsh early-life conditions strongly influenced first-year survival, but that influence fades at older ages. The mechanisms driving trade-offs of poor early-life conditions and future fitness are likely to respond to complex causal routes, and they remain fairly unknown. Thus, we cannot ascertain whether what we observed was the result of compensatory effects, acquired resilience, life-history trait plasticity or a combination of those processes [10,33]. Previous studies suggest that early-life conditions might act as selection filters by eliminating frail individuals from the population, and leading to stabilization of adult survival at high values by environmental canalization typical for long-lived species [14,37–39]. Our results suggest that a strong selection filter operates on this species at least during the first year of life, eliminating those frail individuals, and the strength of mortality during this period depends on the severity of environmental conditions during early life. Therefore, rearing and first winter periods seem to be operating as two consecutive cohort effects, probably resulting in a positive selection for high-quality phenotypes [17].

In our study, food competition by density dependence was a key factor driving the effects of early-life conditions on survival. Breeding gulls intensively exploit trawler fleet discards, and food availability per capita during the rearing period is positively related to improved chick body condition and higher reproductive success [25,40]. We show here that food availability per capita for breeders during rearing also improves future survival of newborns. This cohort effect during the rearing period can be considered a maternal effect because the environment experienced by the mothers influences the future performance of their offspring. After fledging, juveniles disperse and winter in the Senegambia region, where they mainly feed on small pelagic fish shoals [26]. Climatic conditions during first winter also influenced juvenile survival. Positive NAO is associated with the strengthening of the African coast upwelling and increasing the availability of small pelagics [38–40]. Therefore, higher food availability during first winter period improves juvenile survival. Our results agree with our expectations on the survival components of fitness; that is, individuals suffering from food limitation in their early life, during both rearing and first winter, suffer fitness costs [44].

We found that individuals born in years when there was lower competition for foraging resources survived better in their first year of life. When individuals attempt to exploit a common limited resource, competition occurs [45]. The degree of competition depends on both the absolute resource availability and the number of individuals exploiting that resource. Hence, this is a density-dependent process [45,46]. Competition is common in natural populations, and so its effect is implicitly accounted for in most early-life condition studies [16,44]. Such studies include either population size or resource availability as competition proxies and many have found strong density-dependent effects for different fitness components [47–49]. However, we suggest that, when available, the combination 'resource availability per capita' is likely to be a more accurate proxy for density dependence driven by competition. Density-dependent effects on juvenile survival have been widely reported, especially in mammals and birds [2,3,16,50]. These studies suggest that this demographic trait, and particularly first-year survival, is the most affected by density dependence. However, these survival rates are also likely to be the most variable over the years since they have not been environmentally canalized.

Environmentally induced responses are often complex and lead to covariance processes within demographic traits [51,52]. For instance, a decrease in density dependence during rearing increased not only survival rates of gulls (our study), but also the reproductive performance of breeders [22]. These variations in how individuals from different cohorts respond to environmental conditions act as a structuring force in population dynamics, because cohorts of individuals might differ considerably in their future performance [53,54]. The influence of age and environmental variability over the years on several life-history traits and population dynamics has been extensively studied in many taxa, but the potential influence of cohort effects has been seldom considered [55]. For instance, a cohort of individuals reaching sexual maturity synchronously and beginning to breed in a harsh reproductive season can pay a reproductive cost with reduced survival and lifetime reproductive success. Furthermore, the next cohort of offspring could inherit the effects of this bad maternal environment. Thus, we highlight here the relevance of monitoring early-life phases for understanding their sensitivity to environmental conditions and the potential consequences for population dynamics. Although life-history theory predicts that adult survival will be the key parameter driving population functioning, juvenile survival has recently been acknowledged as an important source of variability in population dynamics [17,37,49].

Here, we present the first evidence on how both rearing and first winter conditions shape the survival of the first year of life via density dependence and climate effects. These two consecutive cohort effects synchronously influence the survival of individuals born in the same season and suggest the existence of delayed life-history effects, such as variability and delay in density dependence in population dynamics [54]. The incorporation of these findings into fitness studies and future population models will provide a better understanding of complex population dynamics.

Ethics. This study complies with the current European and Spanish laws regulating scientific research on animals. Permits were given by the Spanish Ministry of the Environment and Delta de l'Ebre NP.

Data accessibility. Data available from the public CEDAI Repository: http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=e13d37f4-2fe6-4f9e-8a51-d60bc6ea1a2c

Authors' contributions. A.P.-P., M.G., A.B. and D.O. collected the data; D.O. conceived the idea, A.P.-P. and R.P. conducted the analyses, A.P.-P. led the writing and A.P.-P., M.G., A.B., R.P. and D.O. co-wrote the article.

Competing interests. We have no competing interests.

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Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers

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Studying colonisation is crucial to understand metapopulations, evolutionary ecology and species resilience to global change. Unfortunately, few empirical data are available because field monitoring that includes empty patches at large spatiotemporal scales is required. We examine the colonisation dynamics of a long-lived seabird over 34 years in the western Mediterranean by comparing population and individual data from both source colony and the newly-formed colonies. Since social information is not available, we hypothesize that colonisation should follow particular dispersal dynamics and personal information must be crucial in decision making. We test if adverse breeding conditions trigger colonisation events, if personal information plays a role in colonisation and if colonisers experience greater fitness. Our results show a temporal mismatch between colonisation events and both density-dependence and perturbations at the source colony, probably because colonisers needed a longer prospecting period to compensate for the lack of public information. Colonisers were mostly experienced individuals gaining higher breeding success in the new colony. Our results highlight the demographic value that experienced individuals can have on metapopulation dynamics of social long-lived organisms.

Species persistence in a changing world depends on the ability to respond to environmental changes[1,2]. A mechanism by which species can cope with such changes is by modifying their spatio-temporal distribution and colonising new environments[2]. Unfortunately, the empirical study of colonisation has been largely anecdotal — mostly in non-social species and through theoretical models[3,4]. Colonisations occur at large spatio-temporal scales and are seldom documented, particularly in long-lived vertebrates[5,6]. Therefore, more information on colonisation processes (e.g., drivers and fitness consequences) and the individual characteristics of colonisers (e.g., experience or age)[5,7] is required.

Dispersal is a multi-step decision process: Individuals must first decide to disperse from their natal or breeding colony; then, individuals must decide between settling in an already occupied site or colonising a new empty patch[8,9]. These decisions require reliable information—anything reducing uncertainty—about the alternatives[10]. Such decisions are more likely to lead to positive outcomes if based on information, reducing uncertainty about the suitability of alternatives[10]. Colonisation is thus a risky endeavour since social information may not be available (or only available through heterospecific habitat copying) and individuals must rely solely on personal information.

Until the 2000's the Audouin's gull (*Ichthyaetus audouinii*) colony at Punta de la Banya (hereafter, source colony) was the most important breeding site hosting up to 70% of the species' world population[9]. During the last three decades, around 20 new Audouin's gull colonies formed along the western Mediterranean providing us with a unique dataset to study patch colonisation. We address three specific questions (1) Do adverse breeding conditions trigger colonisation? (2) Does personal information play an important role? (3) Do colonisers experience greater fitness? We hypothesize that personal information is relevant. We expect to find: (a) a temporal delay

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Site	Habitat	Year	Pairs
Columbretes	Rocky island	1974	45
Punta de la Banya*	Brackish marshes and salt-pans	1981	23
Grosa	Rocky island	1993	300
Albufera	Shallow coastal lagoon	2003	6
El Saler	Artificial coastal lagoon	2004	1
Torrevieja	Salt-pans	2005	30
Benidorm	Rocky island	2006	3
Tomás Maestre	Port	2006	11
San Pedro	Salt-pans	2006	18
Almenara	Shallow coastal lagoon	2009	5
Llobregat*	Artificial riverine island	2010	140
Escombreras	Port	2010	3
Buda	Brackish marshes	2011	1
Castellón*	Port	2011	303
La Ràpita*	Port	2011	2609
Sollana	Shallow coastal lagoon	2012	1
Tarragona*	Port	2013	19
Barcelona*	Port	2013	69
Sant Antoni*	Brackish marshes and salt-pans	2014	116
Valencia	Port	2014	239

Table 1. Names of new colonies formed during the study (see Fig. 1 for location), and their characteristics: type of habitat; year of colonization and number of pairs in the establishment year. New colonies are sorted by year of colonization, except for Columbretes Is, which was likely settled before. Punta de la Banya is the source colony[9]. *Colonies used to assess age structure.

between perturbations triggering dispersal and colonisation (i.e., an amount of time required to explore empty patches and to gather information), (b) that colonisers should be experienced breeders (i.e., previous breeding experience might reduce uncertainty), and (c), since choosing a breeding patch is a risky decision, colonisation should lead to increased population fitness (i.e., higher breeding success)[11].

We searched for qualitative association with adverse breeding conditions by identifying breaking points on the temporal distribution of colonisations. Then, we tested the role of experience in one of three different ways: Firstly, we tested for differences in the proportions of inexperienced and experienced breeders present at new colonies and the source colony. Secondly, we compared the proportion of successful and unsuccessful breeders (BSq_{t-1}) that decided to return and breed again at the source colony or to settle in a new colony. Thirdly, we tested for differences in the laying date (LD), clutch size (CS) and egg volume (V) at the source colony in the year preceding colonisation (t-1) between newly colonizing individuals and philopatric birds (t). Finally, we compared breeding success of a new colony (La Ràpita Port) with the source colony, and specifically with two sub-colonies (i.e., patches) within the source colony with similar age distribution but differing in habitat features related to accessibility for predators.

Results

Since 1981, and particularly since 2003, 19 new colonies were established along the western Mediterranean (Table 1, Figs 1 and 2, see a video of colonisation process in Supplementary Material Appendix 1). We detected high probabilities of breaking points—points that divide data series into blocks such that the mean is constant within each block — in 1992, 2003, 2005 and 2010 (Fig. 2c). This analysis identified three major phases: (a) a 1992 breaking point corresponded with the formation of Grosa colony, (b) colonisation events in 2003 and 2005 coincided with colonisations of six mostly natural sites in the southern part of the study area, and (c) the colonisation of port sites in 2010 (Fig. 1). 37% of the new colonies appeared inside or near ports (Fig. 1). There was no obvious linkage of colonisation events to adverse breeding conditions in the previous breeding seasons (Fig. 2).

In the first year of colonisation, new colonies hosted higher proportions of experienced individuals than the source colony (87.1% and 63.5%, respectively, $\chi^2 = 176.895$, df = 1, $p < 0.0001$). There was no difference in the proportion of previously successful breeders between the new and the source colony in the year of colonisation (BSq_{t-1}, $\chi^2 = 0.739$, df = 1, $p = 0.390$). In other words, settlement colony (source vs. new) was not related to the Q1 breeding success experienced by individuals the previous year (see electronic Supplementary Material S2, Table 2). Colonisers and philopatric individuals also showed similar egg volume, clutch size and laying date in the year before colonisation (see electronic Supplementary Material S2, Table 3).

In the year of its colonisation (2011), breeding success (BSp_t) was higher at the new colony (La Ràpita Port), $BSp_t = 0.31$(95% CI, 0.29–0.34), than at the source colony, $BSp_t = 0.14$ (95% CI, 0.13–0.15), and at both source sub-colonies with a similar age structure to the new colony, $BSp_{tsub1} = 0.24$ (95% CIs, 0.18–0.29) vs $BSp_{tsub2} = 0.1$(95% CIs, 0.07–0.12) (Fig. 3). In 2011, the new colony was free of predation, as was one sub-colony at the source which was surrounded by water (Sub_1), preventing access by terrestrial predators. The other

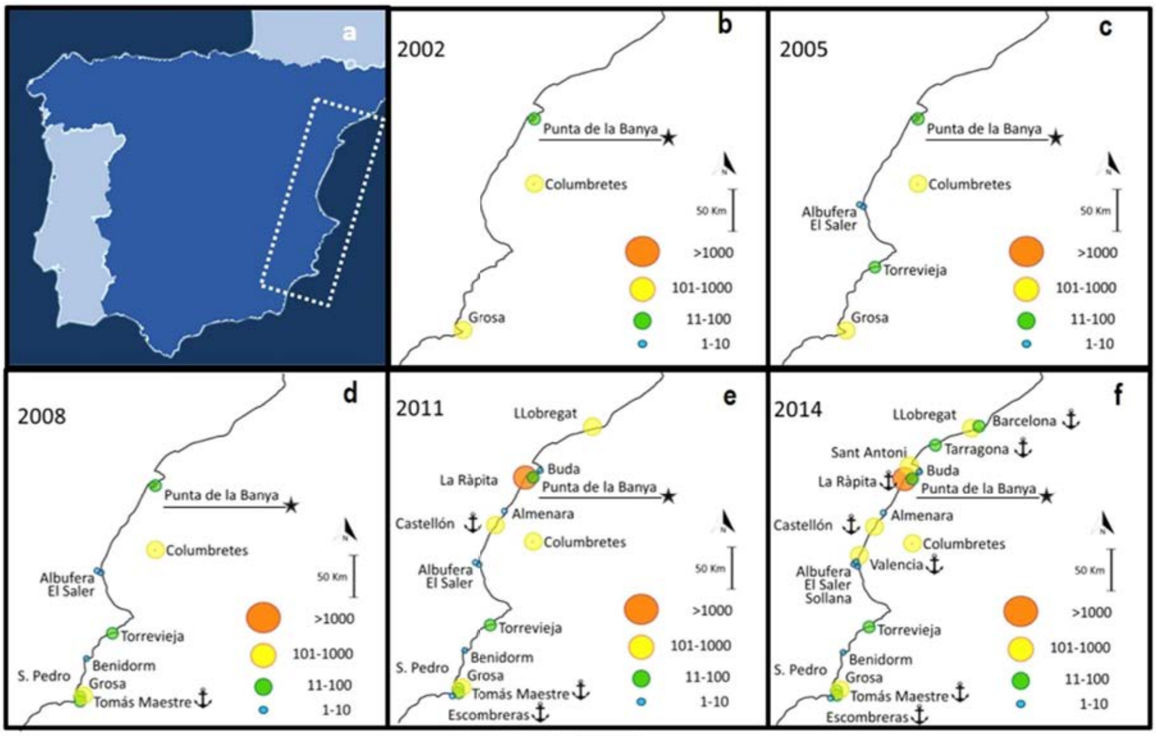

Figure 1. Panel (a) Iberian Peninsula and study area along the western Mediterranean coast (surrounded by white dashed line). We did not include colonies from the Balearic Islands since they have little exchange of individuals with the mainland system[9]. Panels (b) to (f) show the temporal evolution of Audouin's gull colonisation events at regular time intervals from 1975. Circle size is proportional to the number of colonisers in the year of colony foundation; anchors indicate colonies settled in port areas (see Table 1 for colony details). A video with a complete temporal evolution of colonizations is in Appendix S1. Punta de la Banya is the source colony (underlined and marked with a star)[9]. Maps were built in R-Software[38].

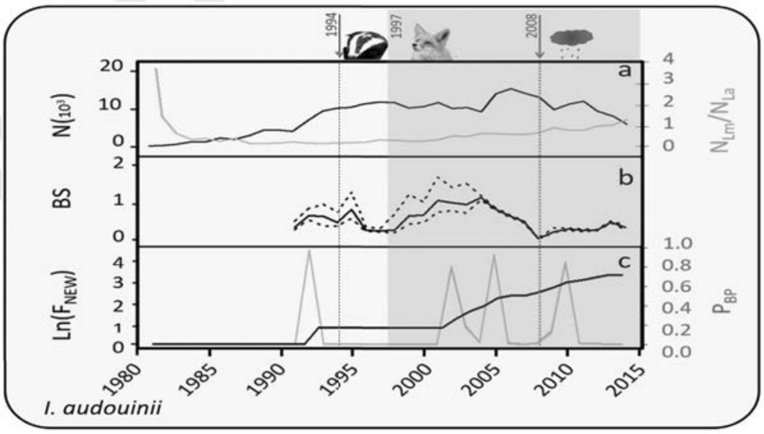

Figure 2. Occurrence of perturbations at *Punta de la Banya* since colonisation (1981–2015): arrows show punctual presence of a badger and an extreme cold storm in different years; shadowed area denotes continuous presence of foxes; Panel (a) Audouin's gull population density fluctuations (black solid line, number of pairs $N * 10^3$); N_{Lm}/N_{La}, ratio of population size between Yellow-legged and Audouin's gulls (grey solid line). Panel b) BS, Audouin's gull breeding success at the *Punta de la Banya* colony (number of fledglings/pair, (95%CI)). Panel (c) Ln (F_{NEW}), neperian logarithm of the accumulated frequency of new colonies by year in the Western Mediterranean (black solid line) and P_{BP}, probability of breaking points for the Ln (F_{NEW}) temporal series (grey solid line). Fox and Badger images were modified from the Flickr photos "redfox10" and "Badger" which are copyright (**c**) 2011 Peggy cardigan https://flic.kr/p/kFvEbZ and (**c**) 2012 Peter Trimming https://flic.kr/p/d5CkEJ respectively. Both images can be used under a CC by 2.0 https://creativecommons.org/licenses/by/2.0/.

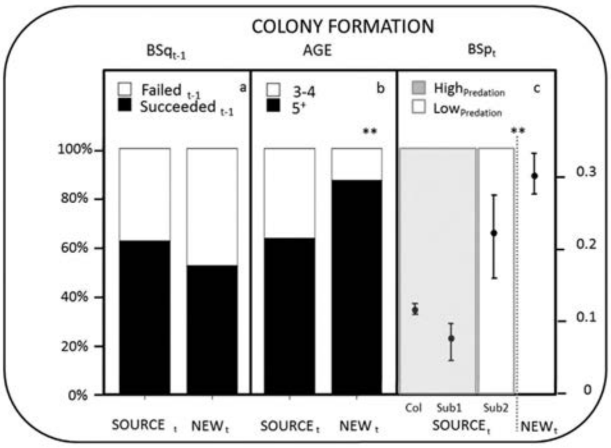

Figure 3. Colony formation patterns for Audouin's gull breeding in the Western Mediterranean. SOURCE refers to individuals present at the Punta de la Banya colony and NEW to individuals present at new formation colonies. Panel (a) represents proportion of individuals present in SOURCE colony and NEW colonies at time t, conditional to their breeding success at t-1 (failed vs succeeded). Panel (b) represents distribution of individuals by means of breeding experience: inexperienced 3–4 years (white) vs experienced 5 years or more (black). Panel (c) represents breeding success of SOURCE colony and NEW colonies at time t with high (grey shadow) and low (no shadow) predation levels. Notice that SOURCE colony includes the average breeding success of individuals breeding at different sub-colonies (patches) at the source colony (Col), and Sub1 and Sub2 are the two sub-colonies within the SOURCE colony with similar age structure to the NEW colony (see Methods) (Sub1, Miseria and Sub2, Alfacs. **$p < 0.001$ significance level).

sub-colony (Sub$_2$), as with many sites at the source colony, suffered from intense carnivore disturbance and predation. Colonies that were more accessible to terrestrial predators experienced lower breeding success (Fig. 3).

Discussion

Colonisation is a crucial process in metapopulation dynamics and may be critical when assessing a species' ability to respond to perturbations[1,2]. Its drivers, the characteristics of colonisers and a quantification of its pay-offs remain fairly unexplored[5,6,11]. Our results show that colonisations seem temporally and spatially unpredictable and they occur in response to an accumulation of perturbations exceeding an unknown threshold. Compared to source colonies, a disproportionate number of colonising individuals were older birds with greater breeding experience. In turn these birds had higher breeding success at newly established breeding colonies.

The temporal mismatch between adverse breeding conditions and colonisations may be in response to several processes which might not be mutually exclusive. First, individuals may face a trade-off between being philopatric, thus taking advantage of their previous experience and colonising a new patch without experience or social information available[10]. At the source colony, higher occupation of sites surrounded by water was likely a behavioural resilience mechanism to mitigate the effects of predation and to avoid the inherent risks of colonisation[12]. This behavioural resilience may delay colonisations of new patches, but it probably has a threshold, particularly when perturbations are consecutive[13,14]. Second, several studies have recorded some individuals visiting empty patches years before breeding, probably to collect information about habitat suitability[10,15–17]. Resilience and philopatry may thus delay the appearance of tipping points in colonisation, and may result in a non-linear relationship between adverse breeding conditions and colonisation[18].

The use of non-natural environments (i.e., ports) appeared as a cultural innovation for the species in the study area, in a similar manner to that which occurred in a naval port in Corsica in 1990[19]. This innovation suggests adaptation to novel environments, and the spread of port colonisations in recent years suggests that colonisers rely on experience and obtain information from already occupied patches to reduce uncertainty[10].

Previous studies at the source colony showed that predation caused partial breeding failure and immediate high dispersal to already occupied patches[13]. Nevertheless, colonisations did not occur immediately after deterioration of breeding conditions. Colonisation seems to follow special dispersal dynamics. Colonisers were experienced individuals that may be followed by young and inexperienced individuals in subsequent years, once the patch is occupied[6,9,16,20].

Colonisation should only occur when advantages of colonisation outweigh its risks[11]. We detected higher breeding performance at the new colony probably due to lower predation risks. Increased fitness should be expected following successful colonisations (i.e., colonies persisting over time); however, that might not always be the case since, given the lack of public information at non-occupied patches, the ability to interpret their suitability is necessarily imperfect[11,13]. Nearly 50% of the new colonies disappeared a few years (or even a single year) after colonisation[21]. Little evidence was available regarding breeding performance during the first years after colonisation events and it did not show a clear pattern[6,20,22].

In summary, we show that breeding experience and longer prospecting periods might be necessary for colonisation. Until now, dispersal theory failed to acknowledge the role of personal information in colonisation for social species[3,4,9]. Future attempts to understand colonisation in social species should focus on how individuals manage and reduce uncertainty when assessing patch suitability[11]. Population models should account for the higher demographic value of experienced breeders since metapopulation dynamics might be more sensitive to those individuals than previously thought. Our results have significant implications for metapopulation ecology but especially for the understanding of how social species respond to environmental change[1,2].

Methods

Audouin's gull is an endemic Mediterranean seabird[5]. Until the mid-2000s, 70% of their world population was concentrated in the Punta de la Banya (source colony, Ebro Delta, 40°37′N, 00°35′E)[9]. However, from 2002 a series of new colonies became established in the western Mediterranean (Fig. 1, Table 1 and electronic Supplementary Material S1). A long-term monitoring and mark-capture-recapture program was established at the source Ebro Delta colony and has been running since 1981, which allowed us to evaluate possible drivers of colonisations[23].

Environmental and breeding performance variables. We used several environmental factors as proxies of adverse breeding conditions: density of aerial nest predators and intra-guild competitors such as the yellow-legged gull *Larus michahellis* (N_{Lm}/N_{La}, yellow-legged gull population size divided by Audouin's gull population size to account for density-dependence)[24]; presence of a single badger (*Meles meles*) that predated on nests in 1994; regular presence of foxes (*Vulpes vulpes*) preying on nests and adults from 1997 onwards; and extreme weather conditions in 2008 (namely, a strong cold storm that killed most chicks)[13,25–27].

Moreover, we also used Audouin's gull breeding success as a proxy of adverse breeding conditions. Breeding success was first calculated qualitatively (BSq), categorizing marked individuals as unsuccessful (0, no hatchlings) or successful breeders (1, at least one hatchling); then quantitatively at a population level (BSp) by dividing the number of chicks by colony size (number of pairs). Number of chicks was estimated by capture-mark-recapture using the Lincoln-Petersen estimator and colony size by counting nests using linear transects[5,28,29]. Breeding success data were available for the source colony and for only one of the newly established colonies (La Ràpita Port).

We considered individual age as a proxy of breeding experience. Most Audouin's gulls in the source colony recruit at the age of 3 and 4. Therefore, we categorized individuals as inexperienced (3–4 years old) vs. experienced ($\geq$5 years old)[30]. Age of individuals was available for 6 colonies in the year of colonization (Llobregat, Castellón port, La Ràpita port, Tarragona port, St. Antoni and Barcelona port) and for the source colony (Punta de la Banya) (Fig. 1 and Table 1). Since the number of individuals colonising each site was commonly low, we lumped resighting data from all 6 new colonies together and compared their age structure with the age structure at the source colony the same years these new colonies were established (2010, 2011, 2013 and 2014, Fig. 1, Table 1).

Finally, as proxies of breeding performance we recorded the breeding phenology (LD, laying date of the first egg as the number of days elapsed since 1st of April, $n = 31$), clutch size (CS, the number of eggs laid by clutch, $n = 50$) and egg volume (V, $n = 50$). Egg volume (in cm^3) was calculated using the equation: $V = \beta\,(L)(W)^2$, in which β was a species-specific constant parameter ($\beta = 0.476$ for Audouin's gull[31,32]), L was egg length and W was egg width, the two expressed in cm. All measures were completed with a digital calliper to the nearest millimetre.

Data analyses. We first assessed the existence of an association between adverse breeding conditions and colonization events. To do this, we calculated the natural logarithm of the accumulated frequency of new colonies over time and searched for breaking points using Bayesian analysis of change point problems implemented in the "*bcp*" R package[33]. Breaking point analyses detects points that divide data series into blocks such that the mean is constant within each block using the Bayesian statistic framework[34]. We then qualitatively assessed if there was a temporal association between the resulting breaking points and different adverse breeding conditions (badger and fox presence and extreme weather events), density dependence (N_{Lm}/N_{La}) and breeding success (BS).

We assessed if there were differences in the proportions of inexperienced and experienced breeders present between the new and the source colony ($n = 827$ and 4810 individuals, respectively) by means of a contingency table and a χ^2 test. We tested the hypothesis that individuals having poorer breeding performance the year before were more likely to colonize a new patch than those experiencing high breeding performance in three different ways. First, we used count data, a contingency table and a χ^2 test to compare the proportion of successful and unsuccessful breeders (BSq_{t-1}) that, having bred at the source colony in the year previous to the colonization ($n = 124$), decided to return and breed again at the source colony ($n = 102$) or to settle in a new colony ($n = 22$). Second, we used individual data and binomial logistic regression (0 = source colony, 1 = new colony) to test the effect of previous breeding status (successful and unsuccessful) as an explanatory variable for colonization. Third we tested differences in laying date (LD), clutch size (CS) and egg volume (V) in the year previous to the colonization (t-1) in the source colony by individuals present at new ($n = 91$) and source colonies ($n = 109$) the year of colonization (t). To test for differences in LD_{t-1} and CS_{t-1} we used linear models, and to test for differences in egg volume (V_{t-1}) we used general linear models including nest identity as a random factor (See ref. 35 for details).

We tested the hypothesis that individuals breeding at new colonies should experience higher breeding success by comparing breeding success at the new colony with breeding success at the source colony the year of colonization. At the source colony, breeding individuals are spatially aggregated in discrete dunes and dikes (i.e., patches)—each of these spatial aggregations is considered a sub-colony which usually has a different age distribution of breeding individuals[36] and habitat characteristics. To eliminate any confounding effect of a different age distribution, we first tested for differences in breeding success with the whole source colony, and then with two sub-colonies (Sub1 called Miseria and Sub2 called Alfacs) within the source colony. These sub-colonies had similar age distributions to the new colony (La Ràpita Port) and differed from one another in their accessibility to terrestrial predators.

Models were selected using the Akaike Information Criterion corrected for overdispersion (AIC_c[37]). We considered the model with lowest AIC_c as the best model, and those within two ΔAIC_c (the difference in AIC_c values) to be statistically equivalent[37]. All analyses were implemented using the R software.

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Author Contributions

A.P.P. conducted the analyses and led the writing; A.P.P., M.G., A.S.A., A.B., J.P., J.G., M.T. and D.O. collected the data and co-wrote the article.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

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Q2 **Ethics statement:** This study complies with the European laws regulating research on animals. Spanish regulation does not require specific ethical approval for wildlife monitoring except from regular permits. Permits were given by Spanish Government: SF/134, SF/043, SF/097 and SF/269.

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VII | Bon viatge

Acknowledgments

Viatge a Ítaca

Kavafis-Carles Riva-Lluis Llach

I

Quan surts per fer el viatge cap a Ítaca, has de pregar que el camí sigui llarg, ple d'aventures, ple de coneixences. Has de pregar que el camí sigui llarg, que siguin moltes les matinades que entraràs en un port que els teus ulls ignoraven, i vagis a ciutats per aprendre dels que saben. Tingues sempre al cor la idea d'Ítaca. Has d'arribar-hi, és el teu destí, però no forcis gens la travessia. és preferible que duri molts anys, que siguis vell quan fondegis l'illa, ric de tot el que hauràs guanyat fent el camí, sense esperar que et doni més riqueses. Ítaca t'ha donat el bell viatge, sense ella no hauries sortit. I si la trobes pobra, no és que Ítaca t'hagi enganyat. Savi, com bé t'has fet, sabràs el que volen dir les ítaques.

II

Més lluny, heu d'anar més lluny dels arbres caiguts que ara us empresonen, i quan els haureu guanyat tingueu ben present no aturar-vos. Més lluny, sempre aneu més lluny, més lluny de l'avui que ara us encadena. I quan sereu deslliurats torneu a començar els nous passos. Més lluny, sempre molt més lluny, més lluny del demà que ara ja s'acosta. I quan creieu que arribeu, sapigueu trobar noves sendes. Bon viatge per als guerrers que al seu poble són fidels, afavoreixi el Déu dels vents el velam del seu vaixell, i malgrat llur vell combat tinguin plaer dels cossos més amants. Omplin xarxes de volguts estels plens de ventures, plens de coneixences.

III

Bon viatge per als guerrers si al seu poble són fidels, el velam del seu vaixell afavoreixi el Déu dels vents, i malgrat llur vell combat l'amor ompli el seu cos generós, trobin els camins dels vells anhels, plens de ventures, plens de coneixences.

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