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Influence of dispersal processes on the global dynamics of Emperor penguin, a species threatened by climate change

Stéphanie Jenouvrier[a,b,*,1], Jimmy Garnier[c], Florian Patout[a,c,d,e], Laurent Desvillettes[e]

[a] Biology Department, MS-50, Woods Hole Oceanographic Institution, Woods Hole, MA, USA
[b] Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS/Univ La Rochelle, 79360 Villiers en Bois, France
[c] CNRS, Univ. Savoie Mont-Blanc, LAMA, F-73000 Chambéry, France
[d] UMPA, Ecole Normale Supérieure de Lyon, UMR CNRS 5669, 46 allée d'Italie, F-69364 Lyon, France
[e] Univ. Paris Diderot, Sorbonne Paris Cité, Institut de Mathématiques de Jussieu - Paris Rive Gauche, UMR 7586, CNRS, Sorbonne Universités, UPMC Univ. Paris 06, F-75013 Paris, France

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ABSTRACT

Species endangered by rapid climate change may persist by tracking their optimal habitat; this depends on their dispersal characteristics. The Emperor penguin (EP) is an Antarctic seabird threatened by future sea ice change, currently under consideration for listing under the US Endangered Species Act. Indeed, a climate-dependent-demographic model without dispersion projects that many EP colonies will decline by more than 50% from their current size by 2100, resulting in a dramatic global population decline. Here we assess whether or not dispersion could act as an ecological rescue, i.e. reverse the anticipated global population decline projected by a model without dispersion. To do so, we integrate detailed dispersal processes in a metapopulation model—specifically, dispersal stages, dispersal distance, habitat structure, informed dispersal behaviors, and density-dependent dispersion rates. For EP, relative to a scenario without dispersion, dispersal can either offset or accelerate climate driven population declines; dispersal may increase the global population by up to 31% or decrease it by 65%, depending on the rate of emigration and distance individuals disperse. By developing simpler theoretical models, we demonstrate that the global population dynamic depends on the global landscape quality. In addition, the interaction among dispersal processes - dispersion rates, dispersal distance, and dispersal decisions - that influence landscape occupancy, impacts the global population dynamics. Our analyses bound the impact of between-colony emigration on global population size, and provide intuition as to the direction of population change depending on the EP dispersal characteristics. Our general model is flexible such that multiple dispersal scenarios could be implemented for a wide range of species to improve our understanding and predictions of species persistence under future global change.

1. Introduction

Rapid climate change poses a fundamental threat to many species because it alters habitat suitability across their entire range. To preserve species in the face of rapid climate change, a new conservation paradigm involving a global spatial scale approach is warranted (Hannah, 2010). To inform conservation and management policy on future climate change impacts, quantitative global population projections including climate effects on population dynamics and forecasts of the future climate are required (Jenouvrier, 2013; Jenouvrier and Visser, 2011).

When the population decline is driven by climate changes that exceed species' tolerance or when acclimation and adaptation are insufficient to allow species persistence in a particular location (Visser, 2008), species' dispersal capabilities could be the key for persistence (Ponchon et al., 2015; Travis et al., 2012). Here, we study whether dispersal will act as an *ecological rescue* mechanism to reverse the global population decline of species endangered by climate change. We distinguish this ecological rescue from the local population rescue effect in source–sink dynamic models (Hanski, 1982). Here, ecological rescue focuses on species persistence, i.e. global population viability.

The Emperor penguin(*Aptenodytes forsteri*, hereafter EP) is an

* Corresponding author.
E-mail addresses: sjenouvrier@whoi.edu (S. Jenouvrier), jimmy.garnier@univ-smb.fr (J. Garnier), florian.patout@ens-lyon.fr (F. Patout), desvillettes@math.univ-paris-diderot.fr (L. Desvillettes).

[1] SJ and JG contributed equally to the study. SJ designed the study, SJ, JG and LD developed the model, SJ, JG, FP performed modeling work and analyzed output data. JG and FP performed the theoretical mathematical analysis, SJ and JG wrote the manuscript, and all authors contributed to revisions.

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Antarctic seabird endangered by future climate change (Jenouvrier et al., 2014), currently considered for listing under the Endangered Species Act (http://www.regulations.gov # FWS-HQ-ES-2016-0072). Previous studies have shown that EPs are very sensitive to change in sea ice, and local and global population declines are projected by the end of the century if sea ice concentration (SIC) decreases at the rates projected by climate models (Jenouvrier et al., 2009, 2012, 2014). EPs depend on sea ice to breed, feed, and molt (Ainley et al., 2010), and there is an optimal amount of sea ice for population growth (Jenouvrier et al., 2012). Because sea ice is projected to decline at geographically heterogeneous rates, some habitats will be more favorable than others (Ainley et al., 2010). Without dispersion, at least two-thirds of known colonies are projected to decline by more than 50% from their current size by 2100 (Jenouvrier et al., 2014). As a result, the global population size is projected to decline dramatically by the end of the century.

Individual dispersal behaviors for EPs are poorly understood because EPs have been marked at only one site (Pointe Géologie, Barbraud and Weimerskirch (2001), Jenouvrier et al. (2005)), and no recapture occurred at other colonies. Until recently, EPs were considered to be highly philopatric (Prevost, 1961). Recent studies have now shown a high degree of genetic homogenization for EP colonies, suggesting high connectivity in these populations via individual dispersal among colonies (Cristofari et al., 2016; Li et al., 2014; Younger et al., 2015, 2017). In addition, recent work suggests that EP colonies can move onto ice shelves and perhaps found new colonies (Fretwell et al., 2012, 2014; LaRue et al., 2015). Thus, there is a current debate on the impact of dispersal processes, and whether dispersion and habitat selection behavior could reverse the anticipated global population decline of EPs.

Dispersal is a process composed of three distinct behavioral stages: the decision to leave the resident patch (emigration), movement between patches (transfer), and settlement into a new patch (immigration) (Bowler and Benton, 2005). Furthermore, individuals may gather and exchange information during these different stages, a process defined as informed dispersal decisions by Clobert et al. (2009). Indeed individuals may preferentially leave unfavorable habitat (e.g. climate deteriorated or exceeding carrying capacity) and settle in higher-quality habitat by relying on environmental cues or by assessing habitat quality through the breeding success or presence of conspecifics (Stamps, 2001). Informed dispersers track environmental conditions closely and concentrate in few favorable patches, while random dispersers "spread their bets" across patches that experience contrasting environmental conditions (Armsworth and Roughgarden, 2005). Several studies have found contrasted results of the effect of informed dispersal on the metapopulation dynamics. Informed dispersal decisions may concentrate the population within few favorable patches, lower the proportion of occupied patches, increasing the probability of extinction of the metapopulation (Anderson et al., 2009; Ray et al., 1991). Conversely informed dispersal decisions may allow the metapopulation population to persist longer at a larger size compared to random or no dispersal by concentrating the population in high-quality habitat (Ponchon et al., 2015). In addition, dispersal distance, landscape structure, local density, and local population dynamics influence species responses to climate change in complex ways (Altwegg et al., 2014; Anderson et al., 2009; Bennie et al., 2013; McRae et al., 2008). Thus, a metapopulation model is required to explore the consequences of various potentially realistic dispersal scenarios on EP persistence under future climate change.

Here, we develop a general metapopulation model that predicts species persistence in heterogeneous landscapes and non-stationary environments arising from climate change. It integrates, in a single framework, three dispersal stages, dispersal distance, informed or random movement, and density-dependent emigration and immigration rates within a structured habitat. Specifically, we incorporate putative dispersal behaviors, and study if the global population dynamics of Emperor penguins depend on 1. the proportion of individuals emigrating from unfavorable quality habitat, 2. the dispersal distance, and 3. the existence of informed dispersal decisions. An 'informed decision' indicates that the decision to leave a colony and resettle is based on both a cue that conveys the climate-dependent quality of the habitat and on the local population density. We discuss how the influence of these climate-dependent dispersal behaviors is mediated by the quality of the whole landscape (measured as the global growth rate), with insights from theoretical models.

2. Materials and methods

We first describe our study species: the Emperor penguin (EP). A metapopulation model is a perfect approach for the EP because they breed in large colonies (> 100 individuals) on fast sea ice (sea ice that is fastened to the coastline), forming a set of discrete, yet potentially connected local populations over the entire species range along the Antarctic coast (Fretwell and Trathan, 2009) (Appendix A, Fig. A.1).

We develop a general metapopulation model including reproduction and dispersal phases that depend on various descriptors of the habitat. We parameterize this model with results of previous studies on the impact of sea ice on EP life history using the long-term capture-recapture data set collected at Pointe Géologie (Jenouvrier et al., 2005, 2010, 2012, 2014), and the spatial distribution of EP colonies observed from satellite imagery (Fretwell et al., 2012). Furthermore, we develop potential dispersal scenarios using information from studies on EP genetic (Cristofari et al., 2016; Younger et al., 2015), foraging ecology (Thiebot et al., 2013), and colonies movement (LaRue et al., 2015), as well as from other birds studies using public information sources (Doligez et al., 2002), and relying on indirect cues to assess habitat quality (e.g. presence of conspecifics (Stamps, 2001)). Finally, we conduct global sensitivity analysis (Aiello-Lammens and Akçakaya, 2016) to assess the respective impact of dispersal distance, dispersion rates and dispersal behaviors on the global population size and to account for high uncertainty in all parameters simultaneously.

2.1. A case study: the Emperor penguin

They reproduce during winter (March through December) on fast sea ice and spend the non-breeding season at sea or on pack sea ice (ice that is not attached to the shoreline and drifts in response to winds, currents, and other forces) (Ainley et al., 2010). Little is known about dispersal behaviors for the EP, thus we construct and compare two models, one which includes dispersal and one which does not. For many seabirds, fidelity to their natal colony and breeding site at adulthood is very high (Gauthier et al., 2010), thus we typically assume that the proportion of emigrant penguins from any favorable colony is zero; this is the basis for the no-dispersal model. We then model a scenario in which the EPs disperse during the non-breeding season. When a site becomes unfavorable, penguins may leave the colony with a probability proportional to their resident habitat quality (informed departure, Clobert et al., 2009). They may settle randomly in a new colony (random search) or in colonies that maximize their fitness (informed search) within their maximum dispersion range. Individuals may disperse over long or short distances using the aforementioned dispersal behaviors.

2.2. The metapopulation model

Our metapopulation model projects the population vector $\mathbf{n}$—comprising the population size n_i in each patch i—from time t to $t + 1$. We write

$$\mathbf{n}(t+1) = \mathbf{D}[\mathbf{x}(t), \mathbf{n}(t)]\mathbf{F}[\mathbf{x}(t), \mathbf{n}(t)]\,\mathbf{n}(t) \quad (1)$$

to indicate that the projection interval is divided into two main phases of possibly different duration: the reproduction phase ($\mathbf{F}$) followed by the dispersal phase ($\mathbf{D}$)[1]. The reproduction matrix $\mathbf{F}$ is constructed using the Ricker model, which includes the intrinsic population growth rate