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Massive and infrequent informed emigration events in a species threatened by climate change: the emperor penguins.

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itory https://github.com/garnieji/EP_demographic_genetic and the code for the importance of climatic and demographic covariates is available from the GitHub repository https://github.com/bilgecansen/Emperor_dispersal.

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Highlights

- Under climate change, dispersal supports persistence but remains difficult to measure.
- New models combining demographic and genetic data unravel dispersal behaviors.
- Emperor penguins leave their colonies when the habitat becomes unsuitable (informed dispersal).
- Emperor penguins experience rare but massive emigration.
- Updated forecasts confirm that penguins are threatened by climate change.

Abstract

Dispersal is a ubiquitous phenomenon which affects the population dynamics and evolution of natural populations, hence it is a fundamental process in driving species persistence under global changes. However, dispersal rates and dispersal range are difficult to measure in most species, and remain unknown for many. In addition, informed behaviors, whereby individuals leave their natal area and select a breeding habitat non-randomly, may play an important role in species' responses to global change, and are even more difficult to comprehend. By developing new models combining demographic and genetic data, we reveal dispersal rates, range and behaviors for emperor penguin, a species threatened by climate change and living in the most remote place on earth where measurements of dispersal are nonexistent. We found that emperor penguins have a short distance of dispersal compared to their capacity to cover large distances during seasonal migration. On average, emigration rates are small, with emigration occurring when the local habitat becomes unsuitable (informed emigration). While overall dispersal rates remain low, occasional mass emigration events can occur in some regions. We also detect environmental and demographic drivers of emigration using new independent data: emigration is more likely to occur for habitats far from open water and with low food availability. Finally, we provided new global population forecasts for emperor penguins that incorporate dispersal processes into a sea-ice dependent demographic model that can inform conservation actions in Antarctica. Our method can be applied to other species and data-poor systems to estimate dispersal processes.

Keywords: dispersal distance | dispersal kernel | dispersal range | emigration rates

1 Introduction

Dispersal characteristics are key in estimating the persistence of species endangered by global change as anthropogenic activities alters habitat suitability across species' ranges [Ponchon & Travis, 2022]. When population decline is driven by global changes that exceed species' tolerances or when acclimation and adaptation are insufficient to allow species persistence in a particular location [Visser, 2008], species' dispersal capabilities could be the key to their persistence [Ponchon *et al.*, 2015; Travis *et al.*, 2012]. However, the rate and range of dispersal of plant propagules and animal individuals are difficult to quantify, especially for endangered species with sparse data or living in remote places on Earth.

The rate and range of dispersal are most commonly characterized by tracking individual movements and population redistribution (e.g using abundance data [Roques *et al.*, 2011] or “mark-recapture/resighting” techniques in animal studies [Turchin, 1998]). However such movement data are extremely challenging to collect, especially for animals in remote ocean environments. Genetic markers naturally present in populations offer unique opportunities to study dispersal [Nathan *et al.*, 2003]. Traditional genetic approaches (e.g. long-term frequency-based approaches using genetic structure described by fixation index) estimate effective dispersal over several generations, rather than dispersal processes relevant for the temporal scales at which ecological and demographic processes occur. Here, we propose a new approach combining genetic methods with demographic models to quantify dispersal rate, range and behaviors of emperor penguins (*Aptenodytes forsteri*), a seabird species living in an extreme environment currently threatened by climate change [Jenouvrier *et al.*, 2021a].

Emperor penguins are identified as the most vulnerable taxon in Antarctica [Lee *et al.*, 2022]. They are the only species to breed on coastal sea ice around Antarctica [Stonehouse, 1952]. If current global warming trends and government policies continue, Antarctica's sea ice will decline at a rate that would dramatically reduce emperor penguin numbers to the

point that almost all colonies would become quasi-extinct by 2100 [Jenouvrier *et al.*, 2021a]. As a consequence, the U.S. Fish and Wildlife Service finalized a rule on Oct. 26, 2022, listing the emperor penguin as “threatened” under the Endangered Species Act. In parallel, the Scientific Committee on Antarctic Research provided substantive scientific justification for designating emperor penguins as specially protected species [Jenouvrier *et al.*, 2021b]. Unfortunately, at the last Antarctic Treaty Consultative Meeting, held in Berlin, Germany in May-June 2022, China blocked the proposal to designate emperor penguins as specially protected species arguing that further science is needed with more research and monitoring of the species. Because dispersal characteristics are unknown for emperor penguins, previous population forecasts assumed a wide range of dispersal scenario, increasing uncertainties in future projections [Jenouvrier *et al.*, 2021a, 2017]. Using our new estimates of emperor penguins dispersal derived from our new likelihood function, we provide enhanced population forecasts of the global population, necessary for informing conservation actions of emperor penguins.

Due to the logistical challenges of monitoring remote populations, very little is known about emperor penguin dispersal behaviors. In fact, emperor penguins have only been marked at one site (Pointe Géologie) [Barbraud & Weimerskirch, 2001]), with no recaptures elsewhere. The recent advent of satellite tracking has allowed for enhanced understanding of emperor penguin movement over large spatial scales. However, this approach is not suitable for ascertaining dispersal between colonies due to the limited life-span of these devices [Thiebot *et al.*, 2013].

Like many seabirds, emperor penguins are considered highly philopatric. However, this traditional view has been challenged with advances in genetic analyses and very high-resolution satellite imagery (VHR) that suggest that movements between colonies occur [LaRue *et al.*, 2015]. Indeed, genetic studies have characterized at least four genetically different clusters that are located in different geographical regions of Antarctica and variously

connected through gene flow, while colonies within each regions appear to be panmictic via dispersal of individuals among colonies [Younger *et al.*, 2017]. In addition, recent work using VHR satellite imagery has documented colony movements, disappearances and relocations [Fretwell & Trathan, 2021]. For instance, a dramatic decline of the world’s second largest emperor penguin colony occurred at Halley Bay, while the nearby Dawson-Lambton colony, 55 km to the south, has seen a more than tenfold increase in penguin numbers during the same period [Fretwell & Trathan, 2019]. Halley Bay has suffered three years of almost total breeding failure caused by a shift in the local environment and sea ice conditions. Those unfavourable conditions may have forced penguins to relocate to Dawson-Lambton [Fretwell & Trathan, 2019]. The colony had been present at Halley Bay since at least 1956, persisting for 60 years before the major environmental perturbation led to a massive population decline and emigration event. This suggests that emperor penguin movements may be triggered by major environmental perturbations and that individuals leave their current breeding site using information about their habitat quality, such as the presence of a stable and suitable ice habitat to breed. These dispersal behaviors correspond to an informed emigration.

To understand the role of dispersal in emperor penguin responses to climate change, demographers have developed a theoretical meta–population model including detailed dispersal mechanisms and stages [Jenouvrier *et al.*, 2017]. It integrates the dispersal distance, density-dependent emigration and establishment rates and dispersal behaviors because individuals may gather and exchange information during these different dispersal stages (informed dispersal decisions [Clobert *et al.*, 2009]). For example, individuals may preferentially leave poor-quality 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]. In parallel, geneticists have assessed emperor penguin genetic population structure using genome-wide single nucleotide polymorphisms (SNPs) [Younger *et al.*, 2017]. Here, by coupling this meta–

population model with those genetic data, we can address the following questions:

1. What are the most likely dispersal behaviors in emigration and establishment of emperor penguins (informed versus random)?
2. What is the mean dispersal distance for this species?
3. What are the emigration rates?
4. What environmental and demographic factors drive emigration rates?
5. How will the global population of emperor penguin change into the future given those dispersal processes?

Methods

Genetic-demographic statistical framework

Based on a mechanistic-statistical approach, we develop a numerically-tractable likelihood function associated with the demographic characteristics of the emperor penguin, including dispersal behavior, mean dispersal distance, and emigration rates per colony, among others (see SI-A for details), given the genotypes $\mathcal{G}_{i,\tau}$ of the sampled individuals.

Genetic structure of the population.

We use genetic data collected from 1993 to 2013 in eight colonies around Antarctica (see [Younger *et al.*, 2017] and SI-A.1). The 110 sampled individuals (10-16 per colony) have been genotyped at the same Λ loci (with possibly some allele frequencies equal to 0). Since emperor penguins are diploids, their genotypes writes $\mathcal{G} = \{(a_\lambda^1, a_\lambda^2)\}_{\lambda=1,\dots,\Lambda}$. Since we use single nucleotide polymorphisms (SNPs), there are two alleles which corresponds to the two possible nucleotide variations of the DNA.

The population of emperor penguin comprises 4 neutral genetic clusters [Younger *et al.*, 2017] characterized by their allele frequencies $\mathcal{F}_{r\lambda} = (p_{r\lambda a})_{a=1,\dots,A_\lambda}$ at each locus λ (e.g.

SNPs), that are assumed constant over the sampling interval because it represents less than two generations for emperor penguins (which is 16 years) [Jenouvrier *et al.*, 2014]).

Antarctica can thus be decomposed into 7 geographical regions (see Fig. 2(b)): 4 regions with genetic information, (WEDD) Weddell sea (Gould Bay to Halley Bay colonies), (MAWS) Mawson Bay (Fold Island to Cape Darnley colonies), (AMPG) Amanda Bay to Pointe Geologie colonies and (ROSS) Ross sea (Cape Washington and Cape Crozier colonies); and 3 regions without genetic data, (StoS) from Smith to Snowhill Island in the Wedell sea colonies, (StoK) from Stancomb to Kloa point colonies and (A-B seas) Ledda bay to Rothschild colonies (Admunsen and Bellingshausen seas) (see more details in SI-A.1)

Meta-population demographic model and dispersal.

We use the meta-population model developed by Jenouvrier *et al.* [2017] to project the population size n_i in each colony i from year to year (see SI-A.2 for details). It incorporate a motionless density-dependent reproduction phase which depends on the habitat conditions (see SI-A.2 for details), followed by a dispersal phase comprising three stages: (1) emigrating from the resident patch at a rate $m_i(t)$, (2) searching for new patch among other patches with an average dispersal distance d (transfer), and (3) settling in a new patch. During the emigration and the searching stages, two possible behaviors (informed versus random) can occur:

- an informed emigration: individuals only emigrate from poor quality breeding sites when the habitat quality is not viable (i.e. negative intrinsic population growth);
- a random emigration: individuals leave the colony regardless of the habitat quality;
- an informed establishment: individuals select the most suitable habitats (i.e. maximize intrinsic population growth) within their dispersal range;
- random establishment: movements are undirected with respect to habitat quality.

In our analysis, we only consider three dispersal behaviors: the random dispersal behavior (R) with random emigration and establishment; the semi-informed dispersal behavior (SI) with informed emigration but random establishment; and the informed dispersal behavior (I) with both informed emigration and establishment.

Computation of the likelihood function.

For the three different dispersal behaviors (random, semi-informed or informed dispersal) and with the unknown parameters Θ , comprising the mean distance dispersal d and the emigration rates $m_i(t)$, of our demographic and statistical models, the likelihood function is:

$$\mathcal{L}(\Theta | \mathcal{G}_{i,\tau}) = \prod_{\tau=1}^J \prod_{i=1}^{G_\tau} \mathbb{P}(\mathcal{G}_{i,\tau})$$

where $\mathbb{P}(\mathcal{G}_{i,\tau})$ is the probability to sample the genotype $\mathcal{G}_{i,\tau}$ in colony τ at time t_i , that can be decomposed as follows

$$\begin{aligned} \mathbb{P}(\mathcal{G}_{i,\tau}) &= \sum_{r=1}^4 \mathbb{P}(\mathcal{G}_{i,\tau} | \text{indiv. } i \text{ belongs to cluster } r) \\ &\quad \times \mathbb{P}(\text{indiv. } i \text{ belongs to cluster } r) \end{aligned}$$

Sampling statistical model associated to the demographic model. The sampling of individuals at a given time t in a colony τ is random among the individuals observed at the colony. Since the average sample size of our data is small compare to the average population size of the emperor penguin colonies, the number of genotyped individuals in τ belonging to cluster r follows a multinomial distribution with parameters G_τ , the sample size, and $(\mu_\tau^1(t_i), \dots, \mu_\tau^R(t_i))$, the frequency of the genetic clusters in the colony τ at time t_i (see detail of this approximation in SI-A.4). The probability that a genotyped individual i observed in colony τ belongs to cluster r at time t_i , is

$$\mathbb{P}(\text{indiv. } i \text{ belongs to cluster } r) = \mu_\tau^r(t_i) = \frac{n_\tau^r(t_i)}{n_\tau(t_i)}.$$

The frequency μ_τ^r corresponds to the ratio between the number $n_\tau(t_i)$ of individuals alive at colony τ , which follows the metapopulation model developed by [Jenouvrier *et al.* \[2017\]](#), and the number of individuals $n_\tau^r(t_i)$, which belongs to the genetic cluster r . Since we are looking at neutral set of loci, the dynamics of $n_\tau^r(t)$ in each colony τ , can be derived from the demographic metapopulation model [[Roques *et al.*, 2012](#)] (see SI-A.3 for details). The genetic and demographic dynamics are linked by:

$$n_\tau(t) = \sum_{r=1}^R n_\tau^r(t) \text{ for each colony } \tau.$$

Statistical genetic assignment approach. Using the linkage equilibrium among loci and the Hardy–Weinberg equilibrium assumption within a cluster, the conditional probability $\gamma_{i,\tau}^r$ for the genotype $\mathcal{G}_{i\tau}$ is:

$$\gamma_{i,\tau}^r = \mathbb{P}(\mathcal{G}_{i,\tau} | \text{indiv. } i \text{ belongs to } r) = 2^{k_i} \prod_{\lambda=1}^{\Lambda} p_{r\lambda a^1} p_{r\lambda a^2}$$

where k_i is the number of heterozygous loci in $\mathcal{G}_{i,\tau}$ and $p_{r\lambda a^1}$ and $p_{r\lambda a^2}$ are the allele frequencies within the cluster r of the alleles a^1 and a^2 of individual i at locus λ (see details in SI-A.4).

For each dispersal behavior, the parameters were obtained by minimizing the logarithm of the inverse Likelihood, that is $-\log(\mathcal{L}(\Theta))$. We performed the minimization with Matlab version R2021a, using a simple Bayesian method, where the prior of the parameters are given in SI-A.5. The code is available online https://github.com/garnieji/EP_demographic_genetic.

Comparison of dispersal behaviors

To assess which dispersal behavior is more likely to occur, we have performed a model selection based on four criteria and our likelihood function: the Bayesian Information Criteria (BIC), two Deviance Information Criteria (DIC) and a predictive Information Criteria (IC)

(see SI-A.6 for detail of computations).

Impact of demographic and environmental factors on emigration rates

For each year, we split the colonies into two categories: "No emigration" colonies when their median emigration rate is 0 during this year and "Emigration" colonies when their median emigration rate is positive. We use a random forest algorithm to quantify the role of several environmental and demographic variables on the emigration probability [Strobl *et al.*, 2007].

We use three demographic factors independent from our meta-population analysis: the size of colony, the growth rate per colony and the frequency of blinking that corresponds to the relative number of years a colony disappears over a period of 10 years, from 2009 to 2018. They were calculated from unpublished data of colony presence and population counts of emperor penguins from VHR satellite imagery [LaRue *et al.*, 2022].

We also considered different environmental variables around each colony, comprising the zooplankton biomass ($\text{mmol } C/m^2$) and the distance between the colony and the nearest edge of fast ice (m). They are obtained using the novel landfast sea ice (hereafter simply "fast ice") data at different scale [Fraser *et al.*, 2021] and the unique sea ice and food web dynamics variables obtained from a forced ocean-sea-ice (FOSI) configuration of the the Community Earth System Model (CESM2) ocean ecosystem model [Long *et al.*, 2021] (see SI-C.1 for details). When applicable, we compute the average value of each variable for different breeding periods: non-breeding (January to March), laying (April and May), incubation (June and July), and chick-rearing (August to December).

We used the R package "party" for fitting the conditional random forests and "permimp" for computing the variable importance scores (see SI-C.2). The codes are available online https://github.com/bilgecansen/Emperor_dispersal.

Forecasts of emperor penguin global population

Coupling our new estimated dispersal parameters with the meta-population model developed by [Jenouvrier *et al.* \[2021a\]](#), we project the total population size of emperor penguin over the century for different climate scenarios labelled by the projected global warming increase ($^{\circ}\text{C}$) above pre-industrial levels: scenario 4.3°C [RCP8.5], scenario 2.6°C [new scenario], scenario 2.4°C [RCP4.5], scenario 2°C [Paris 2°C] and scenario 1.5°C [Paris 1.5°C] (see SI-D for details). The new scenario developed by [Jenouvrier *et al.* \[2020\]](#) is intended to demonstrate probable effects on sea ice and therefore emperor penguins by 2100 if governments act now to control greenhouse gas emissions by 2050.

We compare the outcome of this updated model (semi-informed dispersal), with the projections of the model without dispersal (see Figure 4(a)). Finally, we compare the projections for different dispersal behaviors, and among climate scenarios (see Figure 4(b)-(c)).

Results

Dispersal processes

Our model selection shows that the most likely behaviors supported by the genetic data is the semi-informed dispersal behavior (see Table 1), whereby emperor penguins are likely to depart from colonies with poor habitat (i.e. with negative intrinsic population growth; informed emigration), but settle randomly into another colony (random establishment). Figure 1(a) shows the posterior distribution of the mean dispersal distance for the best supported model, and suggests a short distance of dispersal around 428 km. Figure 1(b), summarizes the emigration rates over the entire continent and supplementary Figure S2 details the emigration rates at each colony. Emigration events are not frequent with a median of zero as more than 50% of the emigration rates calculated at each colony are zero. However, some massive emigration events can occur in some regions and the averaged rate of emigration is not negligible: 15.7% per year.

Figure 2(b) shows that emperor penguins mainly move towards nearby colonies of the same regions with an average rate per year that varies among regions: 15% in colonies of the Amundsen and Bellington seas (A-B seas) to 0.17% in colonies from Smith to Snowhill Island in the Wedell sea regions (StoS) (see Figure S3 for more details). However, massive emigration is also likely to occur between different regions especially between the A-B seas regions and StoS regions (11% to 1.35%) and colonies from Stancomb to Kloa Point (StoKP) and Mawson bay (MAWS) (1.16% to 0.21%).

Potential drivers of dispersal rates

Average emigration rate. First, we found that zooplankton biomass during the non-breeding period (January to March) is the most important variable affecting annual emigration probability among all environmental and demographic variables considered (see Figure 3(d)). Colony size, was the second most important variable influencing the emigration probability (Figure 3(d)) with a positive effect on emigration rate (Figure 3(c)). Despite large uncertainties, the size of the colonies without emigration are almost twice as large than colonies with emigration on average (3,741 penguins versus 1,880 penguins for emigration, see Figure S5).

Annual emigration probability. Secondly, we refine our analysis with only environmental variables by modeling the annual emigration probability. We found that the distance to nearest fast ice edge has a positive effect on the annual emigration probability (see Figure 3(b)), with an importance just after the zooplankton biomass (see Figure S4).

Forecasts of emperor penguin global population

The most likely dispersal processes estimated for the emperor penguins (semi-informed dispersal with small mean distance dispersal 428km and small emigration rates), project a greater global population up to 7% compared with a scenario without dispersion when the climate scenarios lead to large population declines (from scenario 4.3°C and scenario 2°C,

see Figure 4). However, under a climate scenario 1.5°C [Paris 1.5°C] causing lesser declines, our new estimated dispersal processes do not improve the global population size compared to a scenario without dispersion, but may reduce it.

Finally, the impact of dispersal on the future global population size is relatively small compared with the impact of climate change mitigation [Jenouvrier *et al.*, 2021a, 2020] (Figure 4).

Discussion

Using a novel statistical framework combining demographic and genetic data, we found that emperor penguins leave poor habitat colonies but settle randomly into another colony; they show small emigration rates – albeit massive emigration events can occur for some regions – and short dispersal distances. We discuss these novel estimations of dispersal processes in the context of potential individual movements documented via satellite telemetry tags, and colony movements captured via VHR satellite imagery. We note that neither satellite telemetry tags nor VHR satellite imagery allow direct characterization of dispersal rates, distances and behaviors, but are the only information available to date to infer dispersal processes. We integrate this new understanding of dispersal processes to forecast the global population trend for emperor penguins to inform on the species’ designation as a specially protected species.

Dispersal ranges

The posterior distribution of the mean dispersal distance for the best supported model, depicted in Figure 1(a), suggests a short distance of dispersal relative to the potential distance that tracked juveniles and adults cover during their migration [Kooyman *et al.*, 2004; Thiebot *et al.*, 2013]. Indeed, we found that the most likely dispersal distance of the emperor penguins is around 428 km. Satellite telemetry studies have shown that individuals can cover incredible distances during their migration routes. In the Ross Sea, non-breeders can travel up to 9,000

km [Goetz *et al.*, 2018] to their wintering grounds and after the moult adults covered more than 2,000 km on their return journey to their colonies [Kooyman *et al.*, 2004]. In East Antarctica, one juvenile covered more than 7,000 km during the first eight months after leaving its natal colony in Terre Adélie [Thiebot *et al.*, 2013]. However, the distance covered during migration does not necessarily reflect the dispersal distance. Indeed, the potential individual dispersal can be reduced by specific behaviors. For example, seabirds exhibit specific behavioral traits, such as a high degree of philopatry [Aebischer & Coulson, 1990] and the importance of social cues in the recruitment of new breeders [Reed *et al.*, 1999], which may reduce individual dispersal distance relative to potential movement [Kildaw *et al.*, 2005; Matthiopoulos *et al.*, 2005]. For instance, the colonies in the Ross Sea are genetically distinct from the rest of the colonies [Younger *et al.*, 2015], suggesting that, despite their large migration potential during the non-breeding season, emperor penguin dispersal distance could be somewhat limited. In addition, after the demise of Halley Bay, many of the birds from Halley Bay may have relocated to nearby Dawson-Lambton colony, while the formation of new colonies elsewhere or movement to other colony locations further away are considered less likely [Fretwell & Trathan, 2019].

Dispersal rates

Previous studies have debated the magnitude of emigration rates in emperor penguins with some studies arguing for large emigration rates [LaRue *et al.*, 2015], while others for low emigration rates [Mougin & Van Beveren, 1979]. Although some massive emigration events can occur, we found that such events remain rare.

Large emigration rates producing massive movements between colonies have been documented in the past two decades from satellite imagery: 1. Some colonies are known to ‘blink’ (disappear in some years, reappear in others) [Fretwell & Trathan, 2021]; 2. Others are known to relocate onto icebergs or ice shelves during late formation of sea ice in the autumn [Fretwell *et al.*, 2014]; 3. Some colonies have shown dramatic declines whilst the

nearby colonies have markedly increased in size [Fretwell & Trathan, 2019]. Those blinking, relocation and massive movement events remain somewhat infrequent. Spatially, 17% of colonies are known to blink. Some colonies blinked several times in the last decade, so accounting for this temporal variation, there is only a 4% probability that a colony is absent in a given year. In addition, low emigration rates are also expected because a high return rate of marked chicks has been observed at Pointe Géologie ([Mougin & Van Beveren, 1979] and C Barbraud personal communication).

However, it is important to define the temporal and spatial scales at which those rates occur, and here we propose that the averaged annual proportion of individuals moving from one breeding site to another is relatively low for emperor penguins, while en masse emigration may occur occasionally at some locations (see Figure 2(a) and Figure S2). This pattern has been observed in many seabird and bird species, and is coherent with the philopatric behaviour of those species. For example, greater flamingos are long lived and philopatric like emperor penguins. On average they show low emigration rates but when conditions for breeding are unfavorable at their colony (typically low water levels) they move en masse to another breeding site (see [Balkiz *et al.*, 2010; Johnson & Cézilly, 2007]).

In addition, our framework focuses on emigration rates at the population level. However, in many vertebrate species, especially in seabirds, juvenile dispersal is higher than adult dispersal [Clobert *et al.*, 2004]. For emperor penguins, it is likely that massive emigration events consist mainly of adults in some regions while the low background levels of emigration is likely dominated by juvenile dispersal. Further work should include this age structure into the dispersal demographic model in order to disentangle dispersal rates of adults from those of juveniles. However, that would require understanding the detailed mechanisms of density dependence on those two age classes, which are unknown for emperor penguins [Jenouvrier *et al.*, 2012].

Furthermore, when concomitant evolution of both emigration probability and prospecting

occur, the resulting emigration strategy is that successful breeders are always philopatric, while failed breeders are more likely to emigrate, especially when conspecific breeding success is low [Ponchon & Travis, 2022]. In that context, perhaps massive emigration events in emperor penguins consist mainly of failed breeders. Further work could include a breeding stage structure into the dispersal demographic model in order to disentangle dispersal rates among failed and successful breeders.

Potential drivers of dispersal rates

The zooplankton biomass represents the lower food web dynamics of the Antarctic ecosystem and is a proxy for food sources of emperor penguins. We found that it is the most important variable influencing dispersion rates (Figure S4). Indeed, zooplankton biomass during the non-breeding period is negatively related with annual emigration probability (Figure 3(a)). As a consequence, emperor penguins are less likely to emigrate from their colony if resources are abundant prior to breeding.

The fast-ice variables have also an important impact on the probability of emigration. In particular, the distance to nearest fast ice edge has a positive effect on the annual emigration probability (Figure 3(b) and Figure S4). As a result, emperor penguins are more likely to emigrate from their colony if open water is harder to reach. The positive effect of the distance to the nearest fast-ice edge has also been observed on breeding success [Labrousse *et al.*, 2021].

In contrast, we did not detect a strong effect of the demographic factors on the average emigration probability, with the exception of population size (see Fig. 3(d)). Larger colonies exhibit lower average emigration probability (Figure 3(c)) and annual emigration probability (see Figure S5). Even if massive migration events have been observed in Halley Bay due to unfavorable conditions [Fretwell & Trathan, 2019], our analysis shows that the population growth rate and the frequency of blinking do not significantly drive the emigration.

Although more work is needed to elucidate the proximate factors of suitable habitat and

emigration rates of emperor penguins, our results suggest that massive emigration events occur in habitats with low food availability that cannot sustain large populations and in colonies that are distant from open water.

Dispersal behaviors and their consequences for global population dynamics

Our analysis shows that emperor penguins are likely to leave from colonies with poor habitat (i.e. with negative intrinsic population growth; informed emigration), and settle randomly into another colony (random establishment), a behavior referred to as semi-informed dispersal behavior (Table 1).

Previously, [Jenouvrier *et al.*, 2017] have shown that high emigration rates and long distance dispersal accelerate the projected global population decline of emperor penguins and decrease the global population size by 65% by 2100 compared to a scenario without dispersal. However, here we show that high emigration rates and long distance dispersal are unlikely for emperor penguins. We found a relatively short distance of dispersal and low average emigration rates that will slightly increase the global population relative to a scenario without dispersal (see Figures 4(a)-(b)). However, the impact of dispersal behavior, distance and emigration rate on the future global population size is relatively small compared with the impact of climate change mitigation [Jenouvrier *et al.*, 2020] (see Figure 4(c)). At the end of the century, there will be no suitable habitat if greenhouse gas emissions continue their current course, resulting in large global population declines, regardless of dispersal processes [Jenouvrier *et al.*, 2020]. The most important action to ensure refugia for the emperor penguin and halt the dramatic global population decline is to limit temperature increases to well below $2^{\circ}C$ [Jenouvrier *et al.*, 2021a] .

New likelihood function

Many methods have been developed to assess dispersal processes based on genetic data, especially to estimate seed dispersal [Klein *et al.*, 2013]. These genetic methods often rely on

simple dispersal assumptions. For instance, the classical methods (e.g. Euclidian distances or least-cost distances approaches [Broquet *et al.*, 2006]) assume a single direct optimal path for individuals. More realistic approaches including dispersal cost and undirected individual movements during dispersal, have been developed more recently (e.g. resistance networks [Graves *et al.*, 2014]). However, their implementation is challenging and the estimation of dispersal parameters, e.g. by maximum likelihood, generally lacks accuracy [Graves *et al.*, 2013]. Furthermore, those approaches developed for plants and insects, do not account for reproduction and dispersal behaviors that affects the number of individual captured in the different locations.

Recently, new mechanistic-statistical approaches including reproduction have been developed to estimate dispersion of pest species ([Roques *et al.*, 2011] for processionary moth and [Roques *et al.*, 2021] for a bacteria) from genetic data. However, those approaches do not account for temporal variations, nor dispersal behaviors, which is particularly important as some species use personal and social information to decide whether to leave a natal or current breeding site and where to settle (e.g. [Doligez *et al.*, 2002]). Such ‘informed dispersal’ behavior [Clobert *et al.*, 2009] enables individuals to settle in habitats of better quality, potentially improving their fitness, hence increasing population viability and species persistence, especially in the face of global changes [Ponchon *et al.*, 2015]. Here we develop a novel likelihood function that includes informed departure and settlement. Furthermore, this new approach is based on temporal and spatial variations in reproductive behaviors and population dynamics.

To achieve this level of complexity, we assume that the metapopulation is composed of fixed genetic clusters which are at Hardy-Weinberg equilibrium, allowing us to focus only on the evolution of the number of individuals belonging to each cluster. Another possibility for other systems is to compute the dynamics of each allele frequency at any time and any location - a more computationally demanding approach. This dynamic can be modeled by

adapting the methods of [Roques \[2013\]](#), but requires simulating a dynamic system with the size of the total number of alleles in the population, which would be very large in our case study. Another alternative approach might be to use multilocus likelihoods for hybrids and backcrosses developed by [Anderson & Thompson \[2002\]](#). This approach relies on tracking the dynamics of the hybrids at each time step and computing the associated likelihood.

In the present work, we describe the population dynamics of the emperor penguin using a metapopulation model developed by [Jenouvrier *et al.* \[2017\]](#), which comprises the population size in each known colony. Although the local population dynamics account for stage and age structure, the dispersal processes do not, and emigration rates estimated here are averaged at the colony level. Further work entails estimating the emigration rates of juveniles and adults separately and successful and failed breeders separately. Emperor penguin massive emigration events are expected to be driven by adult emigration during unfavourable environmental conditions, while the low background of dispersal may relate to natal dispersal.

Conclusion

In conclusion, using a novel likelihood for a model linking genetic data to meta-population dynamics, we revealed and quantified the heretofore unknown dispersal behaviors, rates and range of emperor penguins. Interestingly, we show that emperor penguins are more likely to depart from poor habitat (informed emigration) with low food resources that can not sustain large colonies. Although this informed behavior suggests that emperor penguins can assess the quality of their breeding site, our study stresses that individuals have a relative poor knowledge of alternative breeding site because they more likely to establish randomly in a new colony. Unraveling those dispersal processes reduce uncertainties in future population projections of emperor penguins necessary for ongoing conservation and management actions.

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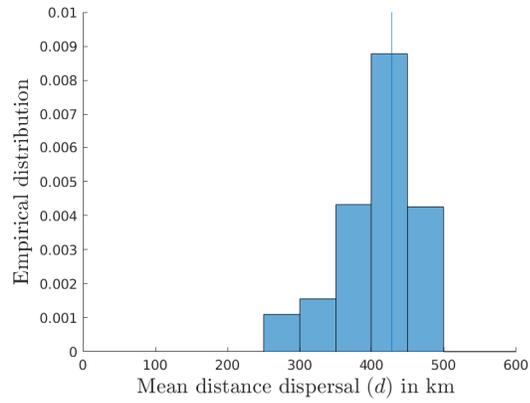
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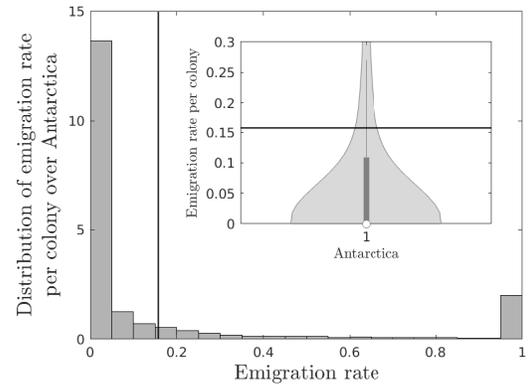
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(a) Mean dispersal distance



(b) Emigration rates over entire continent

Figure 1: Posterior distributions of the mean distance dispersal d per individuals and the emigration rate per colony per year for the entire Antarctic continent. The plain lines are the mean of the distributions: (a) 428 km (blue) and (b) 0.157 (black).

Figures

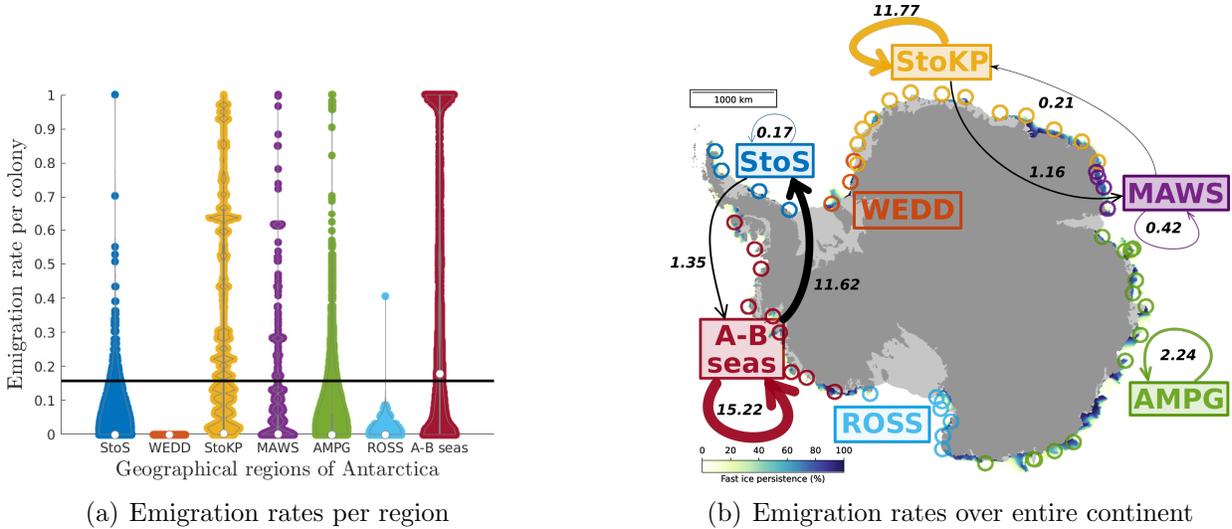
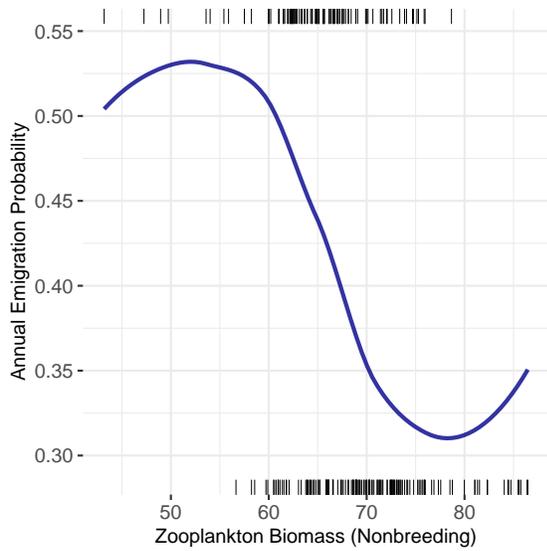
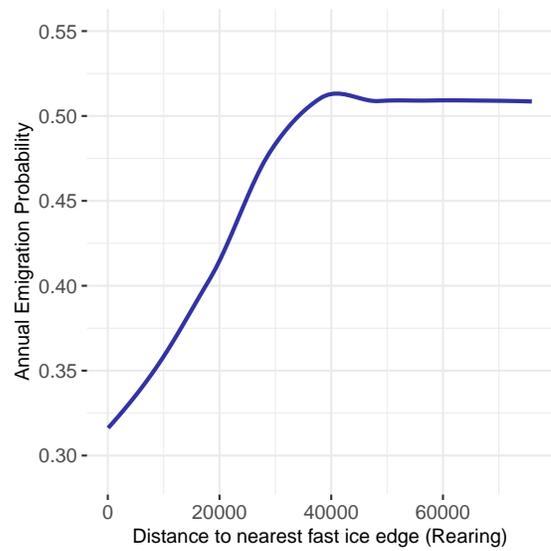


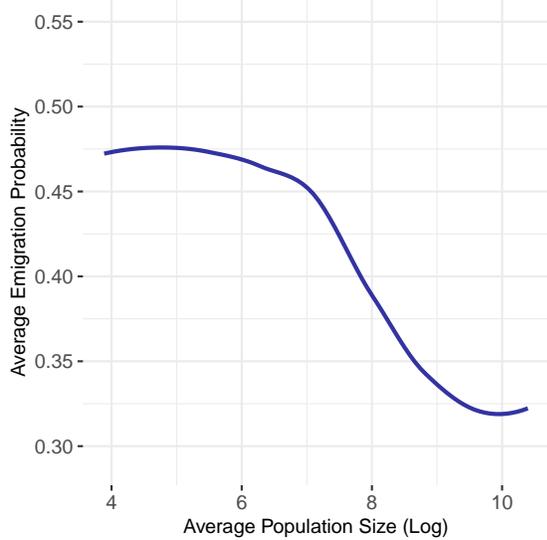
Figure 2: Emigration rates per year per colony (panel (a)) and between and among the seven regions of Antarctica (panel (b)), from 2009 to 2014: from Smith to Snowhill Island in the Wedell sea (StoS), Weddell sea (Gould Bay to Halley Bay colonies) (WEDD), from Stancomb to Kloa point (StoK), Mawson Bay (Fold Island to Cape Darnley colonies) (MAWS), from Amanda Bay to Pointe Geologie colonies (AMPG), the Ross sea (Cape Washington and Cape Crozier) (ROSS) and Admunsen and Bellingshausen seas (Ledda bay to Rothschild Island) (A-B seas). In panel (a), white dots corresponds to the median of the posterior distributions of the emigration rates per colony for each region and the black line is the mean emigration rate for the entire Antarctic continent (0.157). In panel (b), the map background shows the distribution of fast ice persistence, expressed as a percentage of time covering each unit (square of 6.25km) from March 2000 to March 2018 (the map is extracted from [Fraser *et al.* \[2021\]](#)).



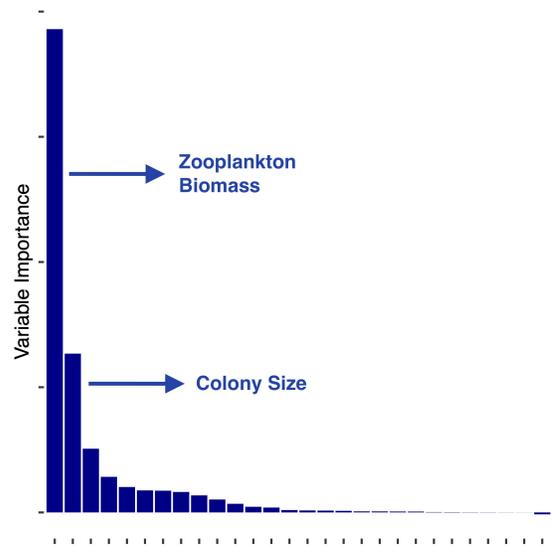
(a) Partial dependence plot for zooplankton Biomass



(b) Partial dependence plot for distance to nearest fast ice edge

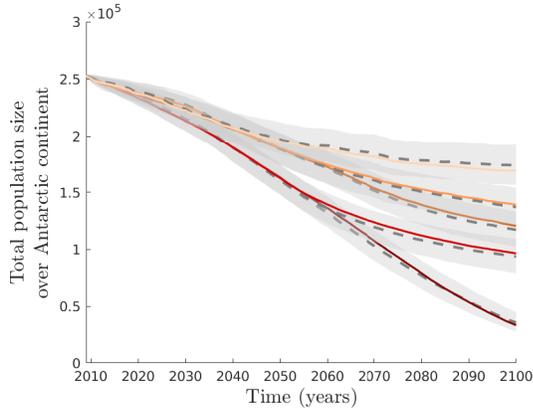


(c) Partial dependence plot for population size

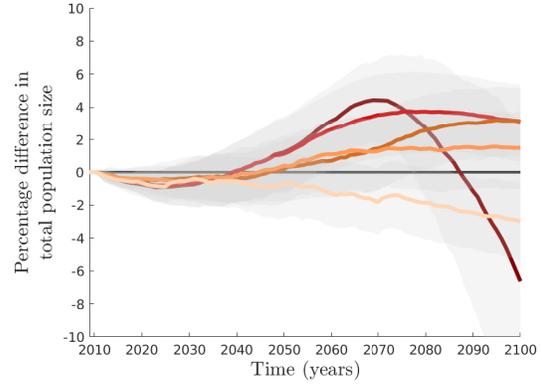


(d) Conditional variable importance

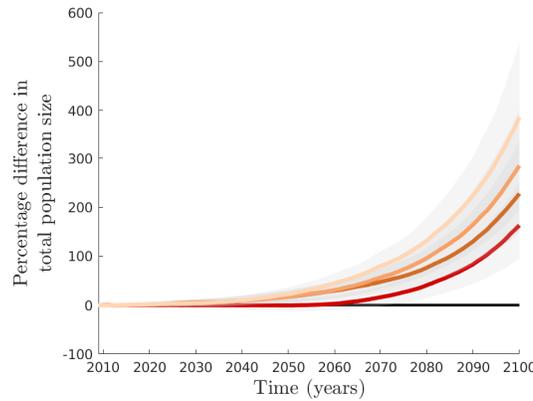
Figure 3: Impact of environmental and demographic factors on emigration rates of emperor penguins. (a) Zooplankton biomass($\text{mmol } C/m^2$) during the non-breeding period (January to March) have a negative effect on annual emigration probability (probability of observing non-zero median emigration rate in a given year and colony); (b) Distance to nearest fast ice edge (meters) have a positive effect. Lines at the top and bottom of the plots show the presence (median emigration rate > 0) and absence (median emigration rate $= 0$) of emigration, respectively, in a given year and colony; (c) Colony size have a negative effect on average emigration probability (proportion of years with non-zero median emigration rates between 2009 and 2013 in a colony); (d) Conditional variable importance scores of random forests modelling average emigration probability. Only the top 2 variables are shown.



(a) Total population size of EP



(b) Difference in dispersal behavior



(c) Difference in climate scenarios



Figure 4: Projection of the total population size of emperor penguin from 2009 to 2100 using the metapopulation demographic model (see SI-A.2) with different climate scenarios. In panel (a), the projected total population size without dispersal (dashed curves) and with semi-informed dispersal with the most likely parameters provided by our analysis (plain curves); The grey regions corresponds to the 1% confident intervals around the median. In panel (b), we present the percentage difference of population size between the projection with a semi-informed dispersal and the projection without dispersal for each climate scenario. In panel (c), we present the percentage difference of population size between the projection with the worst climate scenario 4.3°C [RCP8.5] and the other scenarios.

Table 1: Model selection based on minimization of four selection criteria: the Bayesian Information Criteria (BIC), two Deviance Information Criteria (DIC) and a predictive Information Criteria (IC) for the three different dispersal behaviour: Random dispersal (random emigration and establishment), Semi-Informed dispersal (informed emigration but random establishment) and Informed dispersal (informed emigration and establishment).

Dispersal behavior	<i>BIC</i>	<i>DIC</i> ₁	<i>DIC</i> ₂	<i>IC</i>
Random	678	679	684	674
Semi-informed	-43.6	-828	-41	-1615
Informed	674	605.5	676	535

Table