



# Life history, population dynamics and impacts of cat predation on an endemic gadfly petrel in Cabo Verde

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**ABSTRACT:** Insular fauna often suffers significant predation from invasive mammals, yet robust evidence of their impact from rigorous demographic analysis remains scarce. We aimed to understand the life history and population dynamics of the elusive Cape Verde petrel *Pterodroma feae*, an endemic seabird of the Cabo Verde archipelago, which is severely preyed upon by cats. We analysed capture–mark–recapture data from birds mist-netted in a courtship area in 2007–2021 and monitored their nests between 2012 and 2021 on Fogo Island. Across all islands where this species breeds, we recorded cat predation rates and made additional captures of petrels in courtship areas. Demographic analysis revealed an 8.8% annual population decline of Cape Verde petrels, primarily driven by a 14.7% surplus mortality among breeders from threats in breeding areas, likely tied to the annual cat predation rate of at least 4% observed in monitored nests. Immature males exhibited lower survival rates, likely due to their increased vulnerability while seeking initial nest sites. The limited connectivity detected among and within islands, along with strong nest-site and mate fidelity rates, highlight the urgency of preventing local extinctions, which would be challenging to reverse. This study emphasizes the unsustainability of cat predation rates and the insufficiency of enhancing breeding success to counter the population decline, and it provides compelling evidence of a concerning decline of the Cape Verde petrel, primarily attributable to cat predation. Moreover, it emphasizes the significance of long-term demographic studies to understand the impact of invasive species on endangered populations.

**KEY WORDS:** Population growth rate · Invasive predators · Population viability · Population connectivity · Metapopulation dynamics · Population ecology · Seabirds · Fea's petrel · *Pterodroma feae*

## 1. INTRODUCTION

Understanding population dynamics and trends of imperilled species is a key aspect of conservation biology, as it allows for the identification of factors and processes that could jeopardize population viability (Morris & Doak 2002). This knowledge is crucial for determining the focus of conservation actions, targeting threats that impact the most sensitive demo-

graphic parameters and determining the geographic spread of those actions. In island ecosystems, invasive predators typically pose a major threat to endemic species, often causing rapid and severe declines in native populations (Spatz et al. 2017). Among these predators, cats (*Felix* sp.) are recognized as one of the most destructive, having imperilled or driven to extinction more than 200 bird, 100 mammal and 90 reptile species (Doherty et al. 2016). In insular ecosys-

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tems, free-ranging cats are believed to have contributed to the extinction of 33 species, or 14% of modern birds, mammals and reptiles (Medina et al. 2011). Due to their life-history traits, seabirds are particularly vulnerable to the harmful effects of cats, with impacts currently affecting 90 species, representing 25% of the extant seabird species, a majority of which are globally threatened (Russell et al. 2016, Dias et al. 2019, Rodríguez et al. 2019). Despite the alarming impacts of cat predation, the extent of these impacts has been rarely quantified in demographic studies. Instead, they are often inferred from seabird counts, analysis of cat diets or expert consultation (Bonnaud et al. 2011, Dias et al. 2019). Consequently, robust evidence from demographic analyses remains scarce.

Global population analyses of seabird populations have revealed an alarming overall decline of 70% between 1950 and 2010, with pelagic species exhibiting the most substantial declines (Croxall et al. 2012, Lewison et al. 2012, Paleczny et al. 2015). Half of all albatrosses and petrels are experiencing population declines, with 42% classified as threatened (Rodríguez et al. 2019). Among gadfly petrels, comprising approximately 35 species of the genus *Pterodroma*, these percentages escalate by up to two-thirds, making this group of petrels the second most imperilled group after albatrosses, with numerous populations facing dramatic declines in recent decades (Lascelles et al. 2017). However, due to their secretive behaviour, nocturnal habits, remote breeding sites often located inland in high mountains, and loose coloniality, gadfly petrels are also among the least-known, elusive and challenging-to-study seabirds. Many basic aspects of their biology, such as life history, population dynamics and trends remain poorly understood or entirely unknown for most species. Current assessments of their status are often based on limited or unreliable data (Lascelles et al. 2017).

Gadfly petrels, inhabitants of oceanic islands, have evolved their behavioural, morphological and life-history traits without mammalian predators, rendering them vulnerable to invasive predators such as cats. Invasive alien species at breeding colonies have been recognized as the most severe and persistent threat to this group (Faulquier et al. 2009, Dias et al. 2019). In addition, many gadfly petrels are estimated to have exceedingly small population sizes, making them particularly susceptible to declines. Therefore, there is an urgent need for a comprehensive assessment of their life history, population estimates and trends, particularly in relation to invasive predators.

Gadfly petrels are characterized by their longevity (with a life expectancy exceeding 25 yr) and deferred

sexual maturity (usually >3 yr old). They lay a single egg, which is not replaced if lost, and exhibit extended chick-rearing periods (Brooke 2004, Flood & Fisher 2013, Lascelles et al. 2017). Although annual adult survival rates are available for a handful of species, ranging from 75 to 96% (Brooke et al. 2010, Jones et al. 2011, Ramos et al. 2016, Nicoll et al. 2017, Barbraud et al. 2023), much remains unknown about the mating system and population dynamics of gadfly petrels. Males and females use specific areas for aerial courtship, where they engage in circling flights and rapid dual flights accompanied by sequential singing, leading to pair-bonding in a burrow (Warham 1996). Yet, the fidelity to aerial courtship and nesting areas, as well as the relationship of emigration and immigration between these 2 sites, remains largely unexplored. This gap in knowledge hampers a comprehensive understanding of their connectivity, which could significantly influence population dynamics and, ultimately, impact population viability.

In this study, we focus on the Cape Verde petrel *Pterodroma feae*, an endemic species breeding in mountains on 4 islands within the Cabo Verde archipelago: Fogo, Santiago, Santo Antão and São Nicolau islands (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/n055p187\\_suppl/](http://www.int-res.com/articles/suppl/n055p187_suppl/); for all supplementary material). Currently classified as Near Threatened by the IUCN, the overall population of Cape Verde petrels is estimated at 500–1000 pairs, with trends considered unknown (Hazevoet 1995, Ratcliffe et al. 2000, BirdLife International 2022). Courtship behaviour occurs nocturnally, starting 1 h after sunset, and is characterized by chasing and dual flights mainly during dark, moonless hours (Video S1). These courtship activities typically occur from November to March in specific areas atop certain hills and ridges (Robb & Mullarney 2008). This distinctive courtship behaviour, observed in several gadfly petrel species, presents a valuable opportunity to study population dynamics through mist-netting birds in courtship areas and monitoring nests in the nearby breeding areas. Given the mounting threats facing these species (Militão et al. 2017), conducting a comprehensive demographic analysis to understand the primary drivers of population trends has become an urgent priority (Lascelles et al. 2017).

This study, spanning 15 yr primarily on Fogo Island, Cabo Verde, and more recently extended to all islands where Cape Verde petrels breed, was driven by 2 fundamental objectives. Firstly, we aimed to gain insight into key aspects of the species' life history, including its reproductive strategy, breeding success, survival rates, recruitment mechanisms and connectivity be-

tween islands, breeding and courtship areas. This information served as the basis for constructing comprehensive life cycle and customized demographic models. Secondly, our aim was to estimate population size and to perform a sensitivity analysis to evaluate the primary threats impacting population dynamics and viability, with a specific focus on the impacts of cat predation.

## 2. MATERIALS AND METHODS

### 2.1. Study species

Cape Verde petrels start visiting breeding areas on 24 September and females lay a single egg between 30 December and 8 February. Incubation lasts on average 50 d, with both partners sharing incubation duties by typically performing incubation bouts of about 12 d. Hatching occurs between 26 February and 1 April, and the chick-rearing period lasts on average 3 mo. All chicks fledge before mid-June (Militão et al. 2017).

### 2.2. Fieldwork

This study primarily focused on the aerial courtship area known as Bordeira (altitude of 2053 m) and various nesting sites of *Pterodroma feae* on Fogo Island (Fig. 1). From 2007 until 2021, Cape Verde petrels were mist-netted in Bordeira for about 1 wk annually during the incubation period and early chick-rearing period (January–March). Mist nets were set up at night without tape lure playing (Video S2). Furthermore, from 2012 until 2021, from 2 (when the first breeding area of this species was discovered) up to 38 nests were regularly monitored annually, with breeders and chicks ringed; moreover, annual breeding success and the adults and chicks predated by cats were recorded. Chicks were considered fledglings, i.e. indicating that a nesting attempt was a success, if the chick was alive after 25 April (roughly 2 mo old). Additionally, Cape Verde petrels were captured, marked and recaptured via mist-netting in other aerial courtship areas across Fogo (Fig. 1), Santo Antão,

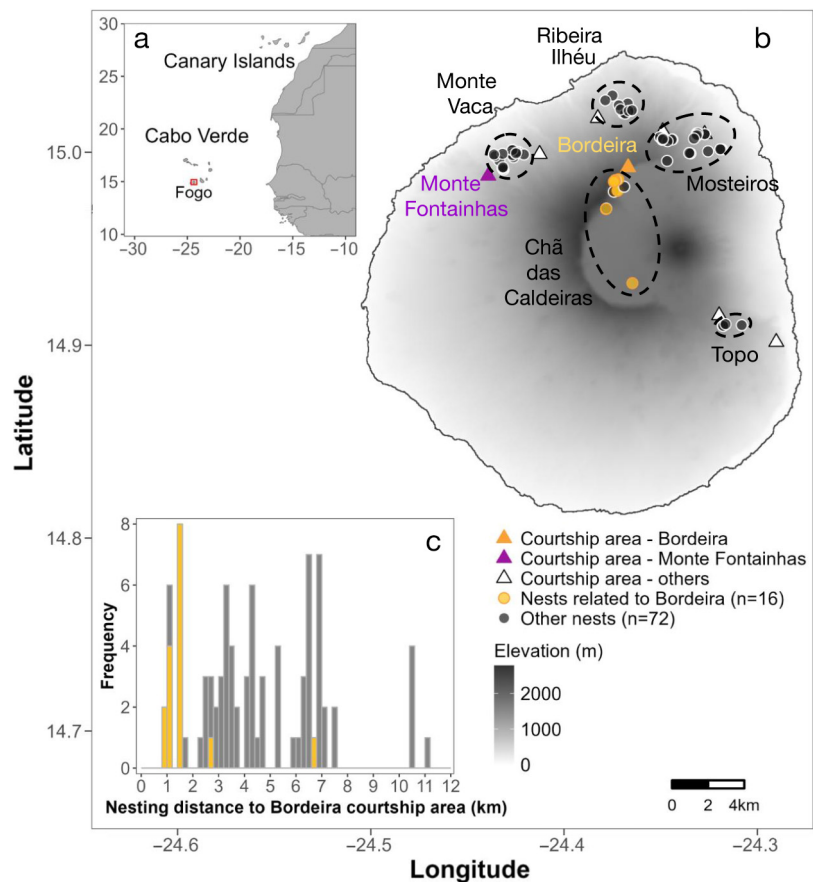


Fig. 1. (a) Fogo Island (red square) within the Cabo Verde archipelago and the Northeast Atlantic. (b) Locations of nests (solid circles) and courtship areas (triangles) of Cape Verde petrels identified on Fogo Island (2007–2021). Mist nets were set in 2 courtship areas: Bordeira (the main study area, yellow) and Monte Fontainhas (purple). The dashed circles represent the main breeding areas: Monte Vaca, Ribeira Ilhéu, Mosteiros, Chã das Caldeiras and Topo. Yellow circles: nests related to the Bordeira courtship areas, i.e. at least one of the adults breeding in these nests was ringed in Bordeira or one of the adults or the chick was ringed in the nest and later recaptured in Bordeira. Dark grey circles: other nests (darker where they overlap). (c) Shortest distance (in km) between each nest and the Bordeira courtship area with the same colours as in (b)

Santiago and São Nicolau Islands from December to April to explore connectivity among courtship areas within and between islands. In 2018, the courtship area of Monte Fontainhas (altitude 848 m) was discovered 7.8 km SW of Bordeira, near the Monte Vaca breeding area (Fig. 1), leading to mist-netting birds in this new courtship area until 2021. Mist-netting also occurred in a courtship area on Santiago Island from 2014 to 2021, while on other islands, mist-netting was conducted at lower and more irregular intensity (2018–2019 and 2021 in Santo Antão Island, and 2019 and 2021 in São Nicolau Island).

Sex was determined for 304, 87, 11 and 91 Cape Verde petrels captured in mist nets on Fogo, Santiago, São Nicolau and Santo Antão, respectively,

through molecular analysis on blood following the procedure described by Militão et al. (2017) or conducted by Sexado de Aves ([www.sexadodeaves.com](http://www.sexadodeaves.com)), a company specializing in molecular sexing of birds.

### 2.3. Breeding status and brood patch

We determined the breeding status of mist-netted individuals based on their brood patch, a specialized area of skin with increased blood flow used to transfer heat to the egg during incubation (Fig. S2). The brood patch develops from early incubation (late December to early February) to hatching (mid-February to late March) (Militão et al. 2017, this study). We examined or photographed the brood patch of almost all mist-netted individuals (missing information on 1.6% captures) using its degree of development from 2 January until 21 March to differentiate between adults and immature individuals (Militão et al. 2017; more details in Text S1 and Figs. S2–S4). For individuals with uncertain brood patch scores or missing data (6.5%), we inferred their age based on their capture history. From mid-March onwards, the brood patch became less informative due to feather regrowth (Fig. S2), and for this reason, the 9 birds mist-netted during this period (in November or December) were excluded from demographic analyses.

### 2.4. Population connectivity

To assess population connectivity, we examined recaptures of Cape Verde petrels on a different island from where they were originally ringed. Movement between courtship areas and nesting within Fogo Island was also verified. To evaluate connectivity between courtship and nesting areas, we calculated distances using the 'distGeo' function in the 'geosphere' package in R (Hijmans et al. 2019). This was done for nests where one individual from a breeding pair had been previously captured and ringed in the Bordeira, as well as for nests where an adult or the chick was ringed at the nest and later recaptured in the Bordeira. Additionally, we estimated nest-site fidelity between consecutive years and 'divorce' rates, as these factors can influence population connectivity.

### 2.5. Cat predation

In Cabo Verde, free-ranging cats are widespread across all inhabited islands and represent the sole

predator capable of accessing burrows and preying on adult Cape Verde petrels (Video S3). Predated petrels were typically found dismembered, forming a broad cushion of feathers up to ~1 m in diameter, with only a few remnants of the animal remaining, particularly the wings (Fig. S5). Thus, those petrels found predated inside, at the entrance or within 10 m of a monitored active burrow (which later failed) were presumed to be part of the monitored breeding population of Cape Verde petrels preyed upon by cats. Occasionally, the legs were found among the remains, allowing us to identify the breeding petrel based on the ring ID. In contrast, those predation events detected far from a monitored active burrow (>10 m) or near fledging dates were not included in the cat predation rate of breeding adults.

### 2.6. Life cycle

A matrix model of the pre-breeding life cycle of Cape Verde petrels (females only) was developed, with 1 yr old birds as the initial stage (Fig. 2a). Drawing from demographic data of Bermuda petrels *P. cahow* from Carlile et al. (2012), we assumed that birds start reproducing between 4 and 8 yr old. Since we did not know the exact age of the birds captured in mist nets, recruitment into the breeder class was modelled as a constant rate, alpha ( $\alpha$ ), representing the probability of an immature bird joining the breeder stage at a given age, conditional on survival. After 8 yr of age, all birds were considered adults and presumed to have bred at least once.

The model accounted for adults breeding or taking 'sabbatical' years, parameterized as breeding (br) and sabbatical (sab) adults. Transitions between these stages were governed by a breeding probability, beta ( $\beta$ ), which was independent of the previous year's breeding status. Survival probabilities varied between stages, with distinctions made for survival during the first year of life ( $\phi_1$ ), young immature birds (1–3 yr old,  $\phi_{1-3}$ ), older immature birds (>3 yr old,  $\phi_i$ ) and adult birds that have bred at least once ( $\phi_{ad}$ ). A surplus mortality, gamma ( $\gamma$ ), was attributed to breeding adults in the nesting area due to increased predation risks, including predation by cats.

Females of the species lay a single egg per season, and fecundity ( $f$ ) represents the probability of a nesting female successfully laying, incubating and rearing a female chick until fledging, assuming sex ratio parity at fledging. A matrix model based on these vital rates facilitated a sensitivity analysis of the population growth rate on the vital rates. Eigenvalue decomposi-

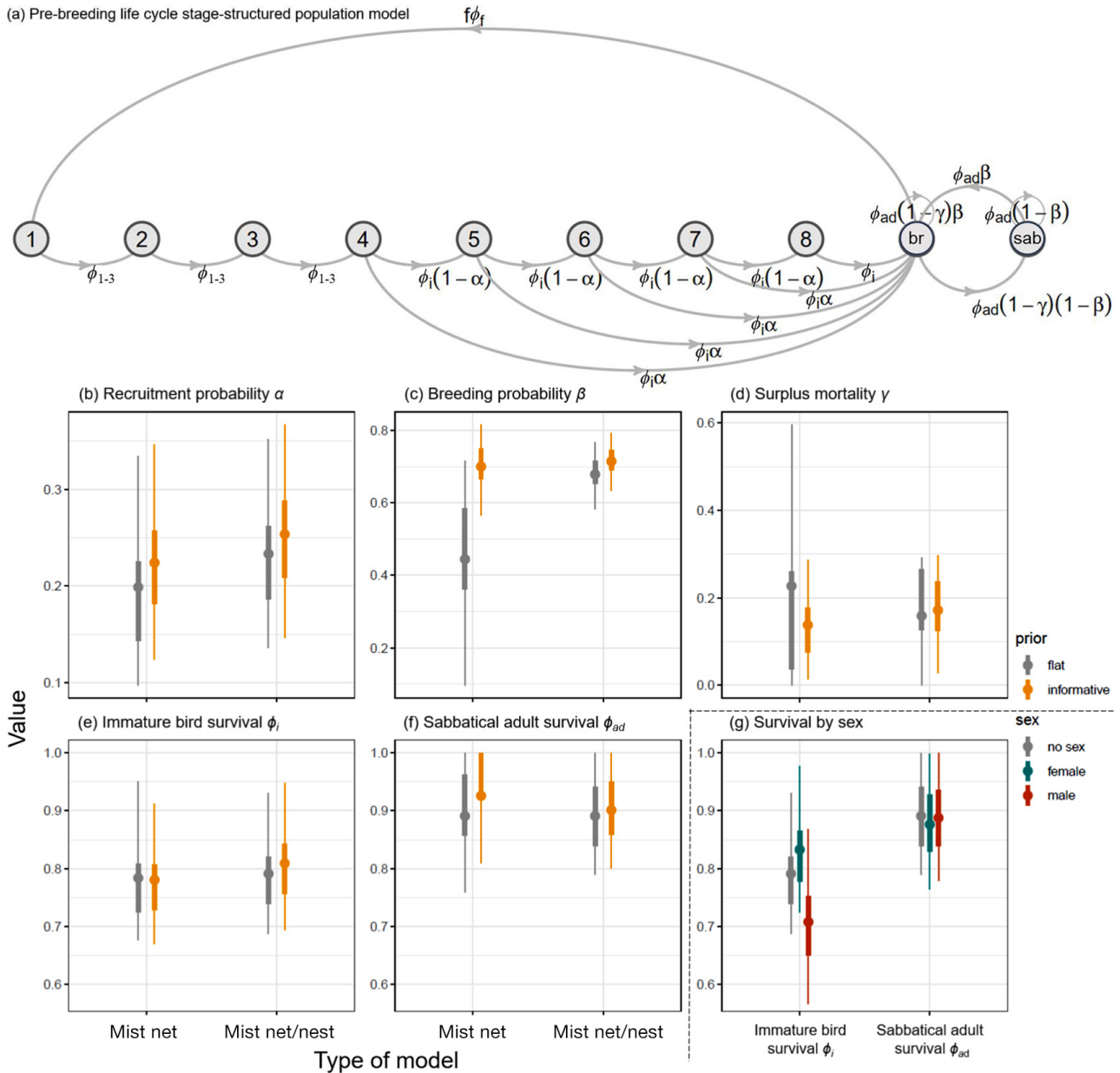


Fig. 2. (a) Pre-breeding life cycle stage-structured population model based on 10 stages. (b–f) Median estimation and 50 and 95% highest posterior intervals of posterior distributions of vital rates from Bayesian models constructed using mist net only or mist-net and nest data with a flat (grey) or informative (orange) prior. These models do not include sex segregation. (g) Median and 50 and 95% highest posterior intervals of posterior distributions of survival rates of immature birds and sabbatical adults from Bayesian integrated models. These models were constructed using flat priors and with or without considering sex segregation. br: adult breeder; sab: adult in sabbatical year;  $\phi_f$ : survival rate of fledglings;  $\phi_{1-3}$ : survival rate of juveniles (from first to third year);  $\phi_i$ : survival rate of immatures;  $\phi_{ad}$ : survival rate of adults;  $\gamma$ : surplus of mortality;  $\alpha$ : probability that an immature bird starts breeding, i.e. recruitment rate;  $\beta$ : probability that an adult breeds in the following year;  $f$ : fecundity rate. Numbers from 1 to 8 represent the age (in years) of immature birds before recruitment. We considered that after 9 yr of age, all birds were adults and had bred at least once. We assumed that when Cape Verde petrels are breeding, they are not captured in the mist net (unobservable state)

tion of the resulting stage-structured transition matrix,  $\mathbf{A}$ , provided growth rate (lambda,  $\lambda$ ) and stable stage distribution (Caswell 2001). Deterministic mean matrix models were analysed with the R package

'popbio' (Stubben & Milligan 2007). Uncertainty in growth rates was approximated by sampling from the posterior distributions of the estimated vital rates obtained through Bayesian analysis (see Section 2.8).



### 2.7. Population size estimate of non-breeding petrels

The population size of non-breeding (i.e. immature birds and sabbatical adults) Cape Verde petrels in the Bordeira was estimated based on birds ringed or recaptured in mist nets, excluding those captured in nests due to birds' fidelity to their burrows (Warham 1996). Given the study duration (2007–2021), we estimated the population size of non-breeding petrels using the Jolly-Seber open population model with the POPAN formulation (Cooch & White 2019). The analysis, conducted using Mark version 9.0 (White & Burnham 1999) through the 'RMark' package (Laake 2013), required testing the goodness-of-fit with a fully time-dependent Cormack-Jolly-Seber (CJS) model using U-CARE version 3.3 (Choquet et al. 2009, 2020) through the package 'R2ucare' in R (Gimenez et al. 2018). The POPAN formulation estimates 4 demographic parameters: apparent survival probability ( $\phi$ ), capture probability ( $p$ ), probability of entrance into the population ( $b$ ) and super-population size ( $N$ ). The super-population size is defined as the total number of individuals in the population during the study period (Crosbie & Manly 1985). These probabilities could be time-dependent or constant through time, denoted by subscripts 't' and '.', respectively. Model selection was based on the value of Akaike's information criterion corrected for small sample sizes (AICc) (White & Burnham 1999). Additional details on the POPAN method and model selection can be found in Militão et al. (2017). The derived estimates of the population size of the non-breeding petrels for each year are also presented.

### 2.8. Estimation of vital rates

To estimate vital rates for the demographic model, fecundity ( $f$ ) was determined by applying a Bayesian binomial model to successful nests at the Chã das Caldeiras site (Fig. 1), with comparisons made to other nesting areas using a binomial mixed-effect model in the 5 breeding areas shown in Fig. 1, using the 'glmer' function in the 'lme4' R package (Bates et al. 2015). For this analysis, we excluded 2014 and 2016, in which, due to logistic issues, only successful nests were registered.

Survival rates for fledglings ( $\phi_f$ ) and young immature birds ( $\phi_{1-3}$ ) were adopted from estimates of other gadfly petrel species, set at  $\phi_f = 0.79$  for fledglings (Brooke et al. 2010, Nicoll et al. 2017) and  $\phi_{1-3} = 0.84$  for 1–3 yr old birds (Jones et al. 2011). Immature and

sabbatical adult survival, surplus mortality among breeding adults, recruitment rate and yearly breeding probability were derived from capture–mark–recapture (CMR) histories for mist-netted individuals using CJS models (McClintock et al. 2020). Bayesian evaluation of models allowed for informative priors and integration of CMR data with nest monitoring data. The data set included 189 capture histories of sexed petrels captured for the first time in the Bordeira from 2007 to 2020 and recaptured until 2021, which corresponds to 83% of the petrels ever captured in Bordeira during the entire study period. Of these 189 capture histories, 157 petrels were ringed in Bordeira as immature birds and 26 as adults. Additionally, 2 birds were ringed as breeders and 4 as chicks at their nests. The state transition matrix included 4 states (immature birds, sabbatical adults, breeding adults and dead). Since birds detected as breeders in a burrow in a certain year were never mist-netted in that year in any courtship area over the entire study period, breeding adults were assumed not observable in mist-netting areas. In contrast, sabbatical adults (birds on a sabbatical year due to e.g. 'widowing' or 'divorcing') were captured in mist nets. Therefore, breeding adults faced an apparent surplus mortality ( $\gamma$ ) due to several threats, including cat predation, to which the sabbatical adults were not exposed. Thus, the apparent survival for breeding adults was  $\phi_{ad}(1 - \gamma)$ , i.e. multiplying the survival rate and the complement of the apparent surplus mortality. In the model using only mist-net data, although breeding adults are not directly observed during the breeding period, the model infers their survival by using data on state transitions and the full capture history of each bird. The transitions between observable states (immature, sabbatical) and the non-observable breeding state, combined with information about subsequent recapture in mist nets or death, allow the model to estimate the survival rate of breeding adults indirectly. Recruitment rate of immature birds was modelled as an age-independent probability ( $\alpha$ ) due to the lack of age information. The probability for an adult individual to breed in a given year was estimated as  $\beta$ . State transitions were modelled as:

	I	Sab	Br	Dead
I	$\phi_i(1 - \alpha)$	0	$\phi_i\alpha$	$1 - \phi_i$
Sab	0	$\phi_{ad}(1 - \beta)$	$\phi_{ad}\beta$	$1 - \phi_{ad}$
Br	0	$\phi_{ad}(1 - \gamma)(1 - \beta)$	$\phi_{ad}(1 - \gamma)\beta$	$1 - \phi_{ad}(1 - \gamma)$
Dead	0	0	0	1

where I represents immature birds, Sab represents sabbatical adults, and Br represents breeding adults.

The observation process was modelled with a time-dependent capture probability  $p_t$  equal for immature birds and sabbatical adults:

	seenI	seenSab	notSeen
I	$p_t$	0	$1 - p_t$
Sab	0	$p_t$	$1 - p_t$
Br	0	0	1
Dead	0	0	1

where seenI stands for observed (i.e. captured) as an immature bird and seenSab means observed as a sabbatical adult.

Capture histories were modelled with and without sex information, focusing on sexed individuals, enabling comparison of model fits. Both flat and informative priors were applied to  $\beta$  (probability of breeding) and  $\gamma$  (apparent surplus mortality affecting breeding adults) to incorporate expert knowledge and the analysis of nest data. Of the 93 nests monitored continuously for 3 yr, 149 instances provided potential for detecting a sabbatical period, yet only 13 occasions revealed inactivity, suggesting a breeding probability ( $\beta$ ) of 0.91 (95% CI 0.86–0.95) through binomial regression, which is consistent with an estimate of 0.89 for Hawaiian petrels *P. sandwichensis* (Brooke et al. 2010).

The mean yearly cat predation rate was 4% (Table S1). Informative prior models used Beta (20,3) (mean: 0.87) for  $\beta$  and Beta (2,10) (mean: 0.17) for  $\gamma$ , while flat prior models employed uniform flat priors for all parameters. Bayesian models integrating mist-net capture histories with nest monitoring data were conducted to refine estimates of common parameters ( $\beta$ ,  $\gamma$  and  $\phi_{ad}$ ). Nest occupancy data were also modelled as a hidden Markov model conditioning on first detection (i.e. the year that a nest started to be monitored), with state transitions defined as:

	Br	Sab	Dead
Br	$\phi_{ad}(1-\gamma)\beta$	$\phi_{ad}(1-\gamma)(1-\beta)$	$1-\phi_{ad}(1-\gamma)$
Sab	$\phi_{ad}\beta$	$\phi_{ad}(1-\beta)$	$1-\phi_{ad}$
Dead	0	0	1

We assumed perfect detection (i.e. the state of a nest burrow as being active or not was known with certainty), so that the observation matrix was:

	Seen	notSeen
Br	1	0
Sab	0	1
Dead	0	1

In sum, we pitted models with 'sex vs. no sex', 'flat priors vs. informative priors' and 'mist net only vs. mist net and nest data'.

The analysis utilized the R package 'nimble' 1.0.1 (Nimble Development Team 2023) for running all models, with code for CJS models referencing Kéry & Schaub (2011). Each model was run with 3 chains of 50 000 iterations, including 5000 burn-in iterations and a thinning rate of every third sample. Chain convergence was verified visually and with the Gelman-Rubin statistic ( $\hat{R}$ ) maintained at or below 1.01. Model comparison relied on the widely applicable information criterion (WAIC). Parameter posterior distributions from Bayesian models were represented as medians and 50 and 95% highest posterior intervals using the 'MCMCvis' package (Youngflesh 2018). Additionally, the proportion of individuals in each stage of the population was calculated. All analyses were conducted in R version 4.3.0 (R Core Team 2023).

### 3. RESULTS

From 2007 to 2021, we captured and ringed 809 Cape Verde petrels (79 chicks and 730 adults): 512 in Fogo, 138 in Santiago, 143 in Santo Antão and 16 in São Nicolau (Table 1). At Bordeira, we captured and ringed 219 individuals and recorded 124 recaptures of 85 of these individuals (Table 1; Table S1). Furthermore, at Bordeira, we also recaptured 3 and 5 petrels that were previously ringed as breeding adults and chicks at their nests, respectively. Additionally, at Monte Fontainhas, from 2019 to 2021, we captured and ringed 139 petrels and recorded 35 recaptures of 32 of these individuals, plus a recapture of 1 individual that had been ringed as a chick at its nest (Table 1).

#### 3.1. Connectivity among aerial courtship and nesting areas

In Fogo in 2007, we started mist-netting birds in Bordeira, and in 2019, we expanded our efforts by mist-netting in a second area, Monte Fontainhas, located 7.8 km from Bordeira. Of all birds ringed in Bordeira, only 2.9% (4 out of 139 recaptures) were recaptured in Monte Fontainhas (Fig. 3). Two of these birds were recaptured again in Bordeira; one of them a few months later and the other 1 yr later (Table S2). Out of 297 Cape Verde petrels ringed on islands (both in breeding colonies and courtship areas) other than Fogo, only 1 bird was recaptured in a Fogo courtship area (Fig. 3).

Table 1. Capture–mark–recapture data of all chicks and adults of Cape Verde petrels in different courtship and nesting areas of each island where this species breeds in Cabo Verde, from 2007 to 2021. **Bold:** the first year that we recaptured a bird in a courtship area ringed as a chick in this locality. Recaptures only include the first recapture of each animal per year

Island	Age of ringing	Location type	Location	Years	Number of birds ringed	Number of recaptures	Number of birds recaptured
Fogo	Chick	Nesting area	Fogo	2012–2021	64		
		Courtship area	Bordeira	<b>2014</b> –2020		9	5
	Monte Fontainhas		<b>2020</b>		1	1	
	Adult	Nesting area	Fogo	2011–2021	86	106	51
		Courtship area	Bordeira	2007–2021	219	124	85
			Monte Fontainhas	2019–2021	139	35	32
Santiago	Chick	Nesting area	Serra Malagueta	2015–2017	3		
		Courtship area	Serra Malagueta	<b>2021</b>		1	1
	Adult	Nesting area	Pico Antonia	2018	1		
			Serra Malagueta	2015–2021	31	23	19
		Courtship area	Serra Malagueta	2014–2021	103	33	28
Santo Antão	Chick	Nesting area	Santo Antão	2019–2020	8		
	Adult	Nesting area	Santo Antão	2018–2021	32	23	14
			Chã Dura	2009	3		
		Courtship area	Corda	2019; 2021	21		
			Covadinha	2018–2019; 2021	18	1	1
Desencaminhadinha	2018–2019; 2021	56	7	7			
Esdrogal	2018	5					
São Nicolau	Chick	Nesting area	Fragata	2021	4		
			Pico Agudo	2021	1		
	Adult	Courtship area	Canto Fajã	2019	11		

Up to 19 birds that were first mist-netted in Bordeira were found some years later to breed in Chã das Caldeiras, close to Bordeira, on average 1.5 km from this courtship area (SD = 0.5 km, N = 14 nests). Up to 6 adults that were found nesting in Chã das Caldeiras were recaptured in Bordeira some years later, after a divorce or apparent widowhood (Table S3). Six birds ringed as fledglings in Chã das Caldeiras were subsequently recaptured in the Bordeira and Monte Fontainhas courtship areas: 3 individuals at 2 yr of age, 2 individuals at 3 yr of age and 1 individual at 4 yr of age (Table S2). These results are summarized in Fig. 1 to illustrate the relationship between the Chã das Caldeiras breeding area and the Bordeira courtship area.

We monitored up to 24 and 23 nests within a 3 km radius from the Bordeira and Monte Fontainhas courtship areas, respectively, but to date, no bird mist-netted in one area was found breeding in the other area, despite being only 7.8 km apart. Nevertheless, 1 individual (5502723 in Table S2), ringed in Bordeira in December 2020, was recaptured in Janu-

ary 2021 in a burrow (with no egg) about 2 km from Monte Fontainhas.

### 3.2. Nest-site and mate fidelity at breeding areas

Nest-site fidelity from one year to the next occurred in 79 out of 81 individual events from 39 different birds that were recorded breeding more than once, resulting in 97.5% annual nest-site fidelity (Table S4). In 15 nests where at least 2 breeding events were detected (from 2012 to 2021) and where the ring numbers of both partners were known, partners divorced in 3 out of 24 breeding pair attempts. That is, the 2 partners were found alive in a following breeding attempt; one partner was mist-netted in the aerial courtship area while the other was found at the same nest or at another nest, overall indicating an annual divorce rate of 12.5% (Table S3).

Among the birds caught in the aerial courtship areas and classified as adults based on their brood patch, we



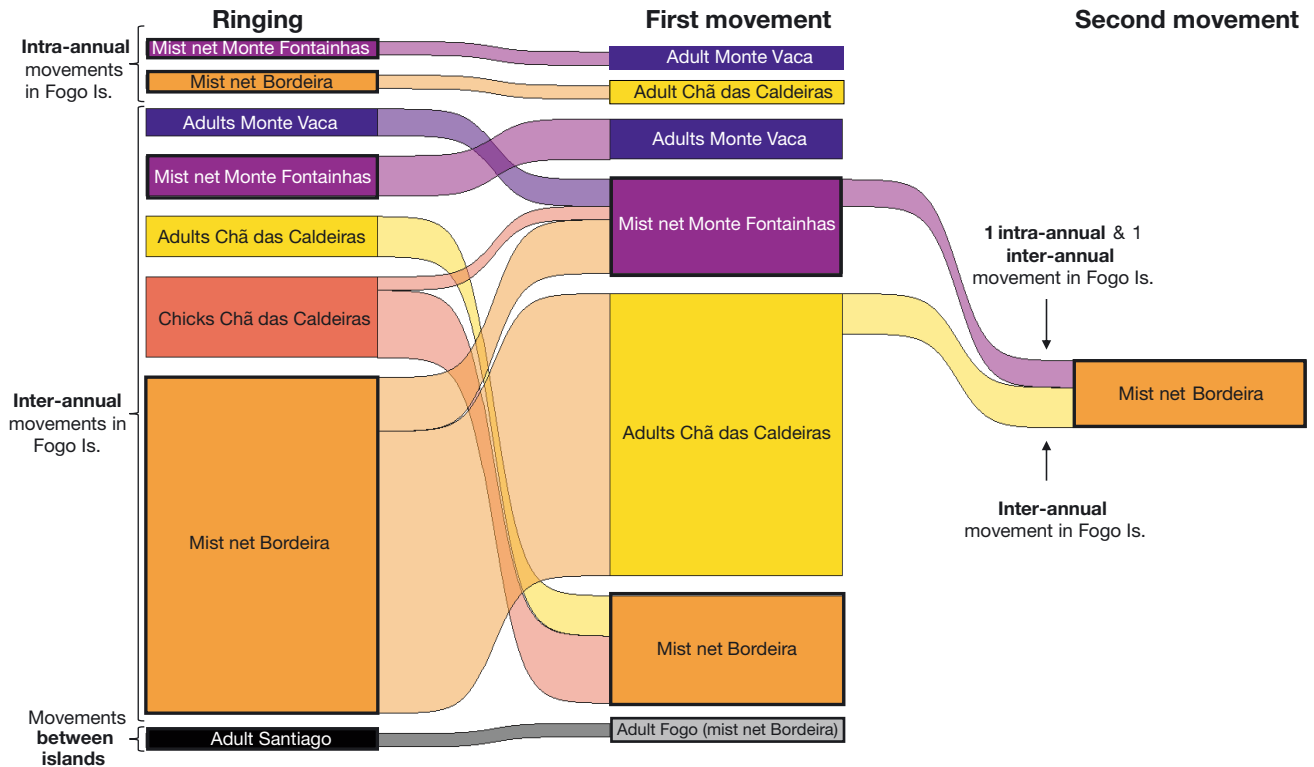


Fig. 3. Inter- and intra-annual movements of Cape Verde petrels between courtship areas, from courtship to nesting areas or vice versa between islands or within Fogo Island. The rectangles represent the areas where the petrels were captured/recaptured and the heights of these rectangles and of the connections between them represent the sample size. Courtship and nesting areas are marked in thick black and thin grey outlines, respectively. Each colour represents a different area. The details of each movement are described in Table S2

could record the previous breeding history for 6 of them. None of them were found breeding that year, with half from known divorced pairs and the remaining birds either divorced from or without partners (the partner was never recaptured or found breeding again and no one was breeding in their nest) (Table S5).

### 3.3. Population size estimated for the Bordeira courtship area

The goodness-of-fit of the CJS model was not significant for the global test ( $\chi^2 = 49.417$  df = 48,  $p = 0.416$ ), so the model fit the data well. The most parsimonious model, i.e. that with the lowest AICc, was the model  $\phi(\cdot)p(t)b(\cdot)$  (Table S6), in which the apparent survival and probability of entrance were constant, and the capture probability was time-dependent. This model reached an AICc weight of 0.994, meaning that it comprises 99.4% of support in the data (Table S6). The rest of the models showed a  $\Delta\text{AICc} > 11$  in comparison with the selected model (Table S6). The super-population size was estimated at  $425 \pm 32$  (SE) non-breeding

petrels (95% confidence interval [CI]: 372–498). The population size per year remained constant at around 100 individuals after the third sampling year (Fig. S6).

### 3.4. Cat predation rates

Overall, from 2017 to 2022, in Fogo, we monitored 163 nests and found 14 adults predated by cats, resulting in an average annual rate of 4.3% of adults predated by cats. Within the same period, we also estimated an average predation rate of 10.0, 0.7 and 3.1% in Santiago, Santo Antão and São Nicolau, respectively. Annual predation rates ranged from 0 to 25%, and the overall rate for Cabo Verde was 4% (Table S7).

### 3.5. Breeding success

Based on the binomial mixed effect model, Cape Verde petrels breeding in Mosteiros and Topo showed lower breeding success than those breeding in Chã das Caldeiras, Monte Vaca and Ribeira Ilhéu

(Fig. 4; Table S8). To obtain the fecundity rate distribution to include in subsequent demographic models (see Section 3.6), we estimated, using a Bayesian binomial model, the annual breeding success of Cape Verde petrels breeding only at the Chã das Caldeiras site (the area with longer nest-monitoring data and nearest to the Bordeira mist-netting area). We obtained an annual breeding success rate of 0.681 with a 95% highest posterior density interval (HPDI) of 0.595–0.764 fledglings per breeding pair.

### 3.6. Bayesian (mist net only and integrated) models and vital rate estimates

Based on WAIC, models using mist-net data only were quite similar, with a difference of slightly over 3 units between the best model (informative priors and sex data) and the worst model (flat prior and no sex). The best 2 models included sex. In contrast, integrated models differed substantially in their WAIC values, with the best model using informative priors and sex (Table 2).

Table 2. Summary of the 2 sets of Bayesian models performed to estimate vital rate parameters of Cape Verde petrels. One set includes only the capture–mark–recapture data obtained from mist-netting, while the other set also integrated the information obtained from nests. WAIC: widely applicable information criterion;  $\Delta$ WAIC: difference in WAIC compared to the best model; lppd: log predictive density component of WAIC; pWAIC: estimate of the effective number of parameters. Model names differ by whether or not they include sex in survival estimates ( $\phi(x)$  vs.  $\phi(\cdot)$ , respectively) and whether they use informative or flat priors (inf vs. flat, respectively). All models included year random effects of capture probability,  $p(t)$ . Models are ordered by increasing WAIC values

Model	WAIC	$\Delta$ WAIC	lppd	pWAIC
<b>Mist-net data models</b>				
$p(t) \phi(x)$ flat	624.64	0	−267.05	45.27
$p(t) \phi(\cdot)$ flat	627.41	2.77	−268.15	45.55
$p(t) \phi(x)$ inf	632.09	7.45	−268.13	47.92
$p(t) \phi(\cdot)$ inf	632.42	7.77	−268.53	47.68
<b>Mist-net and nest data models</b>				
$p(t) \phi(x)$ inf	753.69	0	−328.89	47.95
$p(t) \phi(\cdot)$ inf	753.85	0.16	−329.27	47.65
$p(t) \phi(x)$ flat	759.65	5.96	−332	47.82
$p(t) \phi(\cdot)$ flat	759.91	6.22	−332.39	47.56

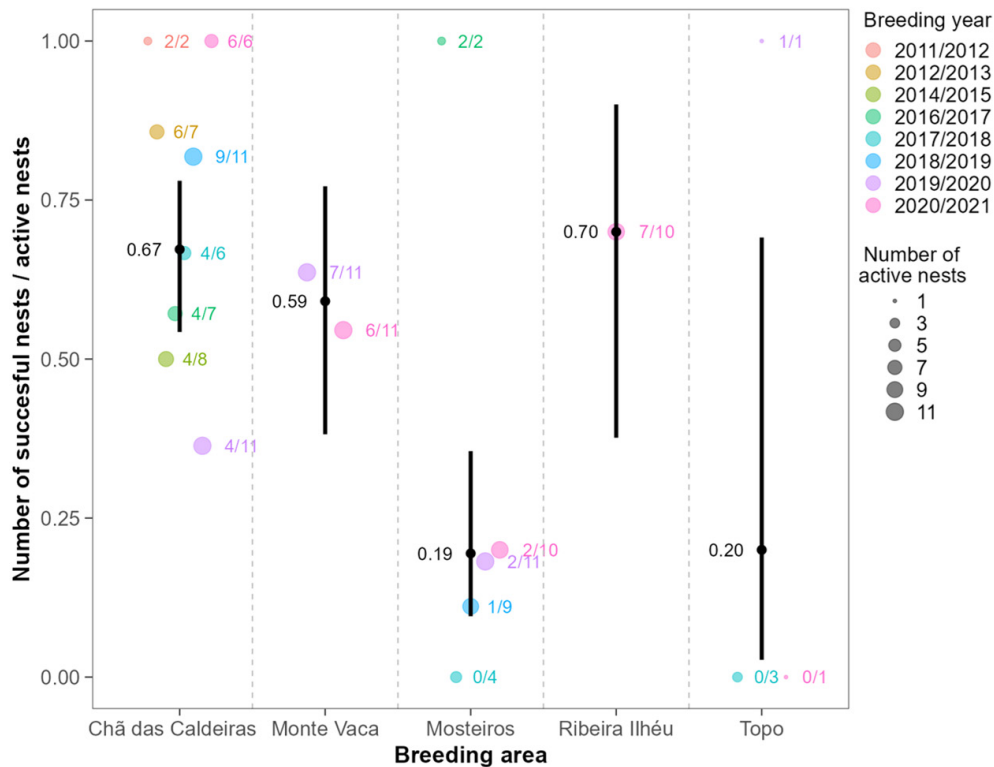


Fig. 4. Estimation of breeding success as the ratio between successful and active nests of Cape Verde petrels in the 5 breeding areas known so far in Fogo Island. The number of successful/active nests per year are presented in different colours depending on the breeding year, and the sizes of the circles represent the total number of active nests in a given area and year. The mean fecundity rate predicted from the generalized linear model is shown in black and the thick lines represent the 95% confidence intervals

Estimates for recruitment probability ( $\alpha$ ), breeding probability ( $\beta$ ), surplus mortality ( $\gamma$ ), immature bird survival ( $\phi_i$ ) and sabbatical adult survival ( $\phi_{ad}$ ) for all models are shown in Fig. 2b–f without sex segregation. Mist-net models with flat priors tended to yield more uncertain estimates than models with an informative prior, in particular for  $\beta$ ,  $\gamma$  and  $\phi_{ad}$ . In contrast, integrated models, which informed parameter estimation with nest monitoring data, yielded more similar estimates regardless of whether informative or flat priors were used, as well as more symmetrical posterior distributions than models using only mist-net data. Also, estimates from integrated models tended to yield estimations that were more in line with those obtained with mist-net data only using informative priors, except for sabbatical adult survival. In the following, only results from selected integrated models will be shown.

Survival estimates for immature birds were lower than sabbatical adult survival across models (Fig. 2e,f). Including sex in the estimation models resulted in similar survival rates for adults but sex differences in survival rates for immature birds, with immature males estimated to be less likely to survive from one year to the next than immature females (Fig. 2g).

Results show that breeding adults are subjected to substantial surplus apparent mortality, with the lowest value estimated at 0.147 (95% HPDI: 0.000–0.230) in the integrated model with sex segregation and flat priors (Table S9). Apparent growth rates estimated from vital rates and the transition matrix are shown in Fig. S7 for the integrated models with uncertainty derived from the parameters' posterior distributions. Estimates were similar and consistently low for all models, with medians below 0.92 in all cases. The highest estimate for growth rate was obtained using estimates from models with sex and informative priors (median: 0.912, 95% HPDI: 0.869–0.955). This estimate for growth rate would mean an annual population decline of 8.8% (95% CI: 4.5–13.1%). The growth rate was especially sensitive to changes in adult survival and surplus mortality while breeding ( $\gamma$ ) (Fig. S8). Indeed, even if we could eliminate the apparent surplus mortality during the breeding season, the median growth rate would not reach the value of 1 needed for the population to remain stable (Fig. S9). For that, it would be necessary to increase the adult survival rate to 0.93 (Fig. 5a). Similarly, even if we increase the breeding success (i.e. the number of fledglings per female and year) to 1, the growth rate

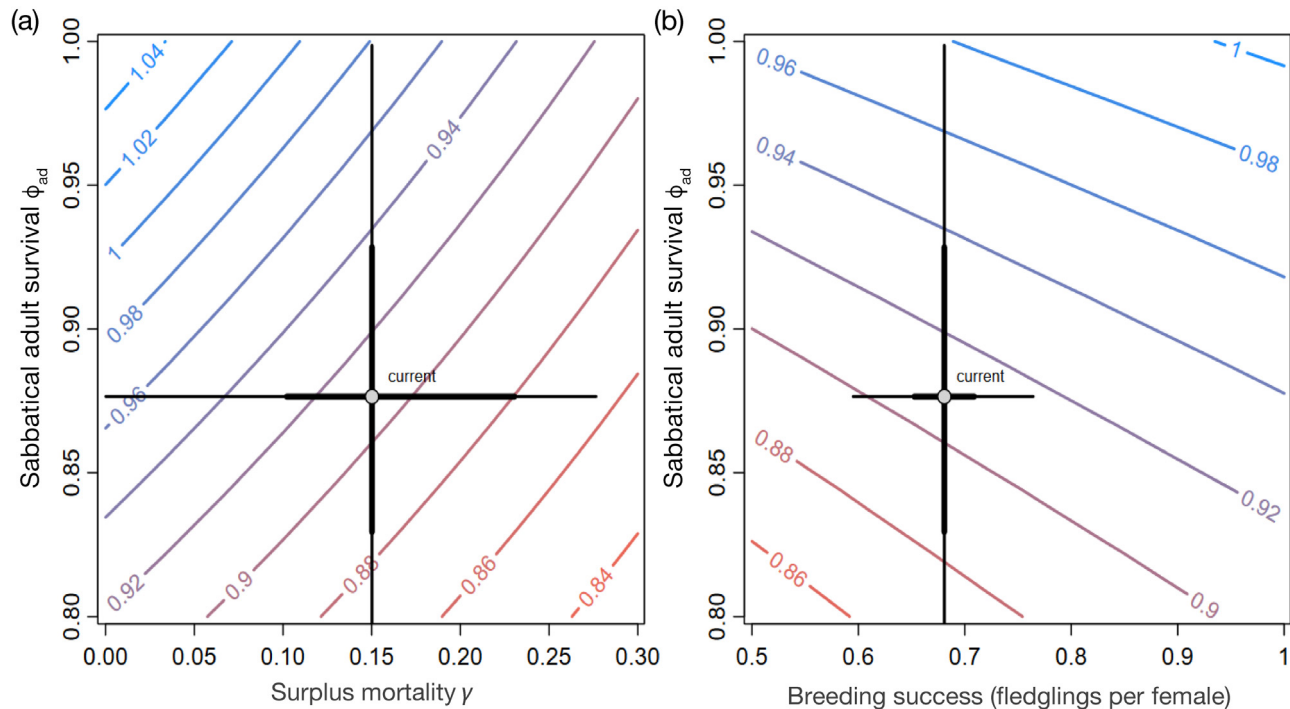


Fig. 5. Prediction of variation of the population growth rate values (coloured lines) depending on (a) changes in sabbatical adult survival (females) and surplus mortality rates and (b) sabbatical adult survival rate (females) and breeding success (i.e. the number of fledglings per female and year). The grey closed circles and thick and thin intervals represent, respectively, the median and 50 and 95% highest posterior density intervals of the parameters estimated from the integrated Bayesian model with the lowest surplus mortality, i.e. the one performed using mist-net and nest data with flat priors and survival rates segregated by sexes (Table S9)

would not reach 1 without increasing adult survival to 0.99 (Fig. 5b).

Assuming a stable stage distribution, our demographic model suggests that the study population comprised 48.6% immature birds, 37.1% breeding adults and 14.3% sabbatical adults (Fig. S10). In the last year of the study (2021), the estimated annual population size for the Bordeira mist-netting area was 105 individuals (95% CI: 80–140) (Fig. S6), which would correspond to 41.83% of the total population (immature individuals aged 3 yr or older and sabbatical adults, Fig. S10), resulting in 93 breeding adults (95% CI: 71–124) in the population associated with the Bordeira courtship area. Note, however, that the POPAN model (used to obtain the annual population size) does not take into account the stage structure of the courtship area population and thus allows only for a rough estimate of the number of breeding pairs.

#### 4. DISCUSSION

This comprehensive study provides valuable insights into the reproductive behaviours, life cycle and population trends of gadfly petrels, with a particular emphasis on the significant threat posed by cats to the Cape Verde petrel population. Through CMR modelling of the Fogo population, our research unveils a concerning decline in Cape Verde petrel numbers, primarily attributed to cat predation. Additionally, the study uncovers limited connectivity between nesting sites and aerial courtship areas, both within and between islands, highlighting the importance of preserving local populations.

##### 4.1. Reproductive strategy

This study represents the most comprehensive investigation to date into the reproductive strategies of gadfly petrels, particularly focusing on fidelity to courtship areas and the interplay between breeding status, courtship areas and nesting sites. Immature birds were found to start visiting aerial courtship areas at 2 to 4 yr old and were typically recaptured over 1 to 3 yr. However, recapture probability at courtship areas drastically declined after this period to less than 0.05 (Fig. S11), suggesting that birds visited aerial courtship areas primarily when seeking a partner, with significantly fewer visits once they reached sexual maturity. Exceptions to this pattern include sabbatical birds, which typically consist of individuals that have recently experienced divorce or widowhood.

The study suggests that birds captured in mist nets primarily comprise immature individuals, with a smaller proportion being sabbatical birds. Consequently, the demographic models were adjusted to treat breeders as unobservable in aerial courtship areas. This adaptation was corroborated by the movement patterns of 5 birds caught at courtship areas that were equipped with GPS/GSM devices during the incubation period, which showed no indication of breeding activity (authors' unpubl. data). Fledglings ringed at colonies near courtship areas were later recaptured as immature birds in the same location. These immature birds typically settled in breeding grounds within a 3 km radius of their initial courtship area, establishing lasting spatial relationships between courtship and breeding areas throughout adulthood. These findings underscore the importance of managing and conserving aerial courtship areas, especially for species like the Cape Verde petrel, whose courtship sites are usually spatially distant from their breeding grounds. Although courting birds do not land in courtship areas, these sites are increasingly threatened by expanding light and noise pollution as Cabo Verde continues to develop. Furthermore, ongoing projects to install cell phone antennas and other infrastructure on hilltops currently used for courtship activities pose a significant collision risk and loss of habitat. Such threats could disrupt or even eliminate courtship activities across large regions, potentially leading to the decline or loss of associated breeding colonies.

##### 4.2. Nest-site and mate fidelity

The study found that Cape Verde petrels exhibit high nest-site and mate fidelity, consistent with other seabirds, including other petrels (Bried & Jouventin 2002, Brooke 2004). There was minimal exchange of individuals between islands, indicating limited natal and breeding dispersal within and among islands, resulting in restricted population connectivity (Danckwerts et al. 2021). This suggests that declines in local nesting areas may not be compensated by immigration from other areas, making local extinctions difficult to reverse naturally (Brooke 2004, Milot et al. 2008, Danckwerts et al. 2021). The observed high nest-site and mate fidelity underscore the urgency of conservation efforts to prevent further declines, as restoring populations from such lows would pose significant challenges. For instance, it took nearly 40 yr to increase the population of the closely related Bermuda petrel *Pterodroma cahow* from just 18 pairs in 1962 to

56 pairs by 2000 (Madeiros et al. 2012), illustrating the lengthy and challenging process of seabird recovery, as also seen in other gadfly petrels (Priddel & Carlile 2007, Gummer et al. 2015).

#### 4.3. Population size estimate

Using CMR data from the Bordeira aerial courtship area on Fogo Island, we estimated the population size of non-breeding petrels. Over the 15 yr study period, the super-population size was estimated at 425 individuals, with an annual population size of approximately 100 individuals (3 yr immature birds or older and sabbatical adults). This corresponds to around 93 breeding adults, or about 47 breeding pairs. The strong attachment of birds to courtship and nearby nesting areas indicates that the estimated population only represents those in Bordeira and its vicinity. Given that we identified at least 8 courtship areas in Fogo (Fig. 1), these results suggest that the Fogo population would be larger. However, this attachment also makes these populations vulnerable to threats like cat predation, which could potentially lead to permanent local extinctions.

#### 4.4. Population growth rate

The median population growth rate, derived from demographic models, indicates an annual 8.8% decline (95% credible interval: 4.5–13%). The estimated time to quasi-extinction, defined as a reduction to below 10% of the current population size, is estimated at 25 yr (95% credible interval: 17–51 yr). Although the annual population size estimated through POPAN analysis may suggest stability, this could be attributed to the inability of the model to factor in temporary emigration (Boys et al. 2019). Underestimation of population growth rates might occur if individuals shift burrows or courtship areas (permanent emigration), which could artificially lower apparent survival and growth rates. However, high fidelity to courtship and breeding areas, along with minimal inter-area movement, implies low permanent emigration rates. In addition, the model relying solely on CMR in mist nets, which would be unaffected by burrow changes, yielded a similar adult surplus mortality as integrated models, suggesting minimal overestimation of adult surplus mortality due to burrow changes. The underestimation of population growth rate may also stem from parameters that we could not estimate directly with our CMR and were instead drawn from the litera-

ture, such as fledgling and young immature survival rates. Sensitivity analysis revealed that the population growth rate is relatively insensitive to fledgling survival but could be notably affected by the survival rates of young immature birds. This highlights the need to refine these survival estimates, as inaccuracies could lead to an underestimation of the population growth rate (Badia-Boher et al. 2024). Despite these limitations, our manuscript identifies critical gaps in current knowledge, paving the way for future model refinements. The predicted significant population decline warrants caution due to model structural uncertainty and data limitations, including the absence of age information and some uncertainty regarding breeding status. Despite these uncertainties, our current knowledge, estimates and models collectively indicate a population decline, potentially offset to some extent by reduced recruitment age.

The predicted decline in Cape Verde petrel populations at the Bordeira site likely extends to other populations across inhabited islands facing similar threats. Models indicate that improving population growth will require enhancing breeding success, immature survival and adult survival. Regarding breeding success, this is mainly impacted by on-land threats, such as predation by cats (Fig. S5 and Video S3) and rats (Fig. S12) or human harvesting (Militão et al. 2017). Despite these threats, breeding success was estimated at 0.68 fledglings per female per year at the Chã das Caldeiras colony, which can be regarded as relatively high compared to other petrels. While there is potential to improve breeding success at some sites, a more comprehensive approach that goes beyond improving breeding success is needed to reverse the predicted downward trend in Cape Verde petrel populations.

Our analysis consistently showed that immature Cape Verde petrels aged 2 yr or older exhibit lower survival rates compared to adults, a pattern commonly observed in many seabird species (Weimerskirch et al. 1997), with some exceptions (Jones et al. 2011). Due to their predominantly aerial courtship behaviour, these immature birds are generally less susceptible to predation by introduced mammals, except during recruitment periods when males search for burrows. Consequently, environmental factors play a more significant role in determining their survival rates. Given the absence of major threats at sea and the limited feasibility of conservation measures to improve immature survival, focusing on this aspect to achieve population stability does not seem practical.

Sensitivity analyses revealed that population growth rates of Cape Verde petrels are highly sensitive to adult survival, consistent with trends observed



in many long-lived seabirds (Weimerskirch 2002). Previous estimates of adult survival for the species ranged from mean  $\pm$  SD of  $0.76 \pm 0.04$  to  $0.80 \pm 0.04$ , but may not be accurate due to the data collection method (Ramos et al. 2016, Militão et al. 2017). These estimates were obtained based on CMR of aerial courtship areas assuming all individuals were adults, which we found to be incorrect because courtship areas are only visited by immature birds and some sabbatical adults. Unlike previous studies, our models separately estimated survival rates for immature birds, sabbatical adults and breeding adults, allowing for more accurate estimations. We found a higher sabbatical adult survival rate, reaching a maximum of 0.90 in integrated models with informative priors and no sex segregation. However, the estimated survival rate for breeding adults was lower at 0.75 (0.70–0.78, 95% HPDI), calculated by multiplying sabbatical adult survival by 1 minus the surplus mortality. Both estimates, particularly for breeding adults, fall well below the mean adult survival rate for procellariiform species, which is estimated at 0.93 (Schreiber & Burger 2002).

#### 4.5. Surplus mortality of breeding Cape Verde petrels

The models revealed a significant surplus mortality rate of 14.7% among adult breeders compared to sabbatical adults, indicating distinct threats affecting breeding adults. Since gadfly petrels are rarely caught as by-catch, the observed surplus mortality is unlikely due to threats at sea (Lascelles et al. 2017, Richard et al. 2020). Instead, Cape Verde petrels face various land-based threats, including light pollution, cat predation and human harvesting (Militão et al. 2017). These threats are likely to affect breeding and sabbatical adults differently, as the latter only come to land for aerial courtship displays. While light pollution is increasing, its impact on grounded birds seems minimal so far (our unpublished data). Surplus mortality may be driven by breeding efforts, but Procellariiformes typically forego reproduction when it becomes too costly, minimizing reproductive costs (Barbraud et al. 2023). Despite the usual trend where reproductive costs affect females more than males (Sanz-Aguilar et al. 2012, Cruz-Flores et al. 2021), our study found no difference in survival rates between breeding males and females. Furthermore, monitoring activities were not found to significantly contribute to the surplus mortality of monitored nests, as the dis-

parity in mortality rates between models with and without nest data was minimal. Cape Verde petrels were historically harvested by humans for consumption and medicinal purposes (Ratcliffe et al. 2000), but such practices have declined due to the scarcity and inaccessibility of nests, as well as reduced use of lanterns or bonfires for capturing these petrels (Semedo et al. 2021). However, cat predation remains a significant threat, primarily impacting breeding adults while sparing those involved in aerial courtship displays, such as the case of the sabbatical adults. The high surplus mortality observed is likely attributed to cat predation, supported by lower survival rates in immature males compared to females, despite the typically stronger natal dispersal of females among birds (Becker et al. 2008, Coulson & Coulson 2008, Barbraud & Delord 2021). Males are particularly vulnerable to cat predation during recruitment periods while searching for suitable nest burrows. For Cape Verde petrels, this typically involves locating suitable cavities that may require further excavation and modification to create a final nesting chamber. In contrast, females generally visit nests that have already been prepared by the males (Imber et al. 2005). This sex-specific behaviour is evident in the declining proportion of males captured at the courtship areas as the breeding season progresses (Fig. S13). Geolocation data further support this difference in burrow-visiting behaviour between immature males and females. Although the data are limited and lack statistical significance, in 2007, an immature female and an immature male were captured in Bordeira and equipped with geolocators. Both were recaptured 3 yr later in the same mist-net area. Analysis of the light data revealed that the female never spent a daylight period in a burrow, while the male spent 1, 2 and 5 d each year, likely preparing a potential burrow for future breeding (our unpublished data).

The discrepancy between the estimated 4% annual average cat predation and the 14.7% surplus mortality likely arises from underestimation. Free-ranging cats may roam inaccessible areas not monitored, and prey consumption away from nests may obscure predation signs. Predation during the pre-breeding period, before monitoring begins, may also be missed. Efforts to identify threats make other significant threats unlikely. On-land threats are linked to rural communities near nesting areas, likely affecting all Cape Verde petrel populations similarly. Thus, addressing cat predation is crucial for conservation, not only on Fogo Island but across all breeding areas and islands.

## 5. CONCLUSIONS

In conclusion, our study underscores the critical role of cat predation in driving the alarming decline of the Cape Verde petrel population, as evidenced by robust demographic analysis. The species faces an ecological trap, continuing to use traditional breeding grounds without adequate management of free-ranging cats. While measures such as rat control and reducing light pollution may offer some improvements in breeding success and population growth, our models stress the pivotal importance of enhancing adult survival to effectively reverse the population decline. Unlike many other petrel species, fisheries pose minimal threats to Cape Verde petrels. Instead, terrestrial threats, particularly cat predation, along with habitat loss for both breeding and courtship, represent the most significant dangers to their survival. The strong philopatry and breeding-site fidelity observed in these birds limit their dispersal potential, making local extinctions a grave concern and hindering population recovery even under favourable conditions. This underscores the urgency of managing the impacts of free-ranging cats, as restoring populations from such lows would be extremely challenging. Given the widespread impact of cat predation across all breeding populations in Cabo Verde, the prospect of numerous local extinctions is significant. Conservation efforts should also include facilitating the recolonization of breeding refuges free of cats, such as through translocation programmes to Santa Luzia Island. This island is currently cat-free and shows evidence of historical petrel occupation (Alho et al. 2022).

Our findings underscore the urgent need for long-term demographic research to fully understand the impacts of cat predation and the imperative to address this threat promptly. Free-ranging cats are increasingly recognized as a major threat to biodiversity, particularly in insular ecosystems, preying on various endemic and endangered species. Therefore, efforts to manage free-ranging cat populations will not only benefit seabirds but also support the survival of numerous other endemic vertebrate species worldwide.

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