



## Original Research Article

## Integrating habitat and partial survey data to estimate the regional population of a globally declining seabird species, the sooty shearwater

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## ABSTRACT

Many animal populations are thought to be in flux due to anthropogenic impacts. However, censusing organisms to understand such changes is often impractical. For example, while it is thought that over half of pelagic seabird populations are declining, most breed in burrows or on cliffs, in large, remote colonies, making them difficult to count. Burrow-nesting sooty shearwaters (*Ardenna grisea*) are abundant but declining in their core (South Pacific) breeding range, potentially due to introduced rodents and habitat loss. In contrast, Kidney Island, their largest colony in the Falkland Islands (Southwest Atlantic), purportedly grew by several orders of magnitude since the mid-1900s. This island is rodent-free, and native tussac grass (*Poa flabellata*) has increased following cessation of historical exploitation. To estimate the sooty shearwater population in the Falkland Islands, and its relationship with breeding habitat availability, we sampled burrow density and occupancy on Kidney Island and modeled these as functions of habitat. Both indices responded positively to a proxy for historical increases in tussac cover. We estimate that breeding sooty shearwaters occupy ~140,000 (95% CI: 90,000–210,000) burrows on Kidney Island. Moreover, using additional survey data and Generalized Functional Response models to account for intra-island variation in habitat availability, we estimate that 25,000 (95% CI: 20,100 – 30,500) burrows could be occupied on nearby islands from which non-native rodents have been recently eradicated. Our study shows that habitat selection functions, generalized where necessary, not only improve population estimates but provide biological insights needed to reverse declines in seabirds and other species.

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## 1. Introduction

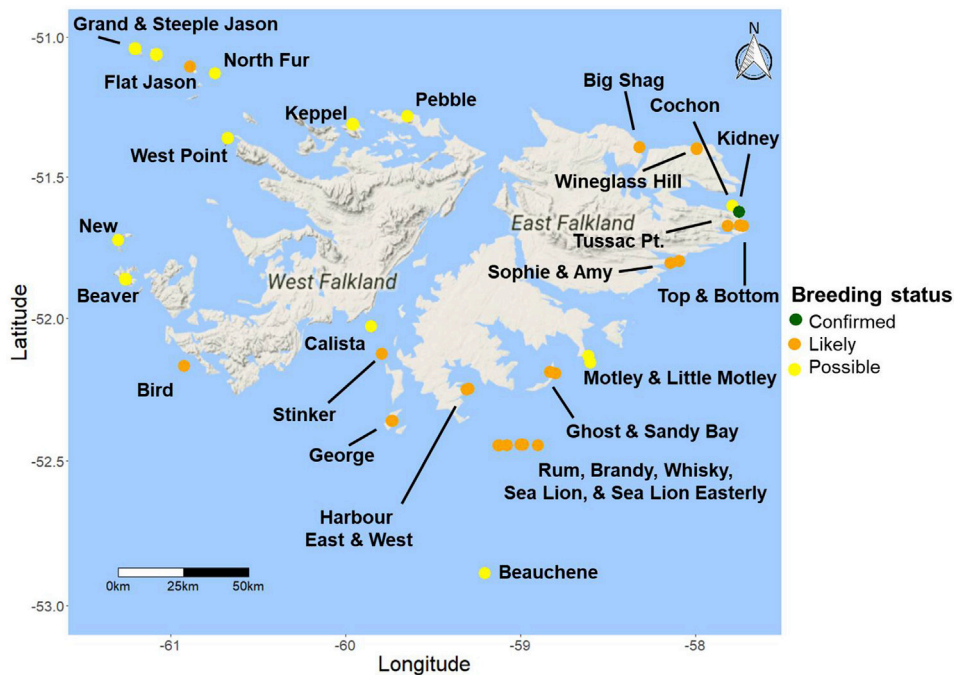
Many animal populations are thought to be in decline due to human activities (Halpern et al., 2008) while others are growing following the alleviation of historical impacts (Buxton et al., 2014). As a result, the structure, function, and resilience of ecosystems are changing rapidly, sometimes in unexpected ways (Baum and Worm, 2009; Estes et al., 2011). In order to detect, monitor, and understand these changes for conservation, accurate and precise population estimates are required. However, it may not be practicable to count organisms directly, either because they are difficult to observe, too numerous, or too widely dispersed. It is common practice therefore to estimate population size based on assumptions about the relationship between species and habitat (Boyce and McDonald, 1999). Simple “design-based” estimation assumes that population size can be estimated by multiplying the density in a subset of randomly placed sample plots by the area occupied. The latter is often defined based on assumptions about what constitutes suitable habitat. However, if these assumptions are wrong the resulting population estimate will be biased. In contrast, by modeling dependencies of population size on resource or habitat availability, for example using habitat selection functions (HSFs), more accurate “model-based” estimates can be made (e.g., Scott et al., 2009). This approach has the additional advantage that important insights can be gained into the factors that drive and potentially limit population size (e.g., Ali et al., 2017). However HSFs fitted to data from one area may predict poorly in other areas if these have different habitat availability regimes (Mysterud and Ims, 1998). Generalized Functional Response models (GFRs), which account for differences in animals’ responses to changes in habitat availability, can be used to overcome this (Matthiopoulos et al., 2011) but GFRs have not yet been applied widely to the problem of population size estimation.

Pelagic seabirds are an important exemplar of these issues. Over half of their species are thought to be declining due to anthropogenic impacts, including introduced predators, fisheries by-catch, habitat loss, and climate change (Croxall et al., 2012; Phillips et al., 2016). Conversely, a few of their populations are increasing, in response either to conservation interventions or natural processes (Buxton et al., 2014). However, relatively few of the world’s pelagic seabird populations are monitored (Croxall et al., 2012), making it difficult to assess these changes or their causes properly. This is partly because seabirds are relatively hard to survey: At sea, they typically range 1000’s to 10,000’s of km, making it largely impracticable to use at-sea surveys to estimate population sizes accurately. It is more practicable to survey breeding colonies, but these are often very large (up to  $10^6$  pairs) and located on remote islands or coastlines. Moreover, within colonies, seabirds often nest on cliffs or in burrows, which they enter or leave only at night (Warham, 1990; Brooke, 2004; Croxall et al., 2012).

Sooty shearwaters (*Ardenna grisea*) are medium-sized burrowing petrels that breed colonially on temperate coasts of the South Pacific and Southwest Atlantic, digging deep and sometimes complex burrows up to 3 m long (Hamilton, 1998; Clark et al., 2018). Although sooty shearwaters are highly abundant (global population ~20 million individuals; Brooke, 2004), they are declining, both at colonies in their core breeding range around New Zealand, in the South Pacific, and in the wintering areas used by birds from this population (Scott et al., 2008; Moller et al., 2009; Waugh et al., 2013). The IUCN classifies sooty shearwaters as “near-threatened” but others have argued that they should be up-listed to “vulnerable” due to the severity of these declines (Scott et al., 2008). These declines have variously been attributed to: Predation by introduced species – principally rodents (Newman et al., 2008, 2010); breeding habitat loss (Jones, 2000; McKechnie et al., 2008); direct harvest (Lyver, 2000; Newman et al., 2010); incidental by-catch (Uhlmann, 2003); and climatic change (e.g., in wind currents and sea surface temperatures; Shaffer et al., 2006).

Contrary to the global trend, sooty shearwaters are thought to be increasing in one area – the Falkland Islands, in the Southwest Atlantic (Otley et al., 2008). Kidney Island (Fig. 1) is by far the largest known colony of the species in the Falklands archipelago (Woods and Woods, 2006). Although it has never been systematically surveyed, periodic subjective estimates suggest that it has grown by two orders of magnitude, from ~2,000 to ~100,000 breeding pairs since the 1950’s (Woods 1988; Woods and Woods, 1996; 2006). It has been hypothesized that this is due to an increase in tussac grass (*Poa flabellata*), which provides the species’ principle burrowing habitat in the Falkland Islands. Historically, tussac was harvested for animal fodder (Falklands Conservation, 2006). Tussac cover was also reduced by intentional or accidental fires but these impacts ceased on Kidney Island in the 1950’s (Carstairs, 1996). Rodents have never occurred on Kidney Island but invasive, non-native populations occur on many of the other Falkland Islands, including small tussac-covered offshore islands, which therefore have low numbers of burrowing seabirds (Hall et al., 2002; Poncet et al., 2011). In order to restore native bird populations, rodents have recently been eradicated from two tussac islands (Top and Bottom) adjacent to Kidney Island and these are now thought to hold small but growing breeding populations of sooty shearwaters (Poncet et al., 2012). Sooty shearwaters are also thought to breed on at least 21 other islands in the archipelago (Fig. 1, Table 1).

Design-based colony surveys of burrowing seabirds (e.g., Olivier and Wotherspoon, 2006; Scott et al., 2009; Pearson et al., 2013) most commonly involve counting burrows in survey plots, calculating the mean density, and then multiplying this by the total area of available breeding habitat (Rayner et al., 2007a; Sutherland and Dann, 2012). However, breeding habitat selection by seabirds is poorly understood making the delimitation of available habitat prone to bias (Bried and Jouventin, 2002). For example, particular types of vegetation cover may facilitate burrow excavation, while steep slopes, facing prevailing winds, might be needed for shearwaters to take off effectively (Scott et al., 2009). However, many crowded but apparently stable seabird colonies are surrounded by unused yet seemingly high quality nesting habitat (Warham, 1990). This indicates either that habitat availability is not limiting or that assumptions regarding habitat selection and suitability are wrong. For example, most seabirds are highly colonial and therefore presumably prefer to nest near conspecifics, perhaps to the extent that otherwise suitable habitat distant from settled areas remain unoccupied (Warham, 1996). Unless modeled



**Fig. 1.** Distribution of known or suspected sooty shearwater breeding sites in the Falkland Islands. Breeding is either considered *confirmed* due to presence of eggs or chicks, *likely* due to presence of burrows (but eggs and chicks have not been seen), or *possible* due to other evidence (see Table 1 for details).

explicitly, this tendency for nesting seabirds to cluster could manifest in unexplained spatial autocorrelation, which in turn would result in an overestimate of accuracy (Olivier and Wotherspoon, 2006). Surveying burrow-nesting seabirds is further complicated because not all burrows may be occupied so occupancy as well as burrow density must be assessed (Rayner et al., 2007a; Parker and Rexer-Huber, 2015). In a growing colony, new burrows may be constructed at the margins in poorer habitat. As such, the dependence of burrow density on habitat may be weaker than the dependence of burrow occupancy on habitat.

We aimed to: (1) quantify how sooty shearwater burrow density and occupancy vary with habitat, including current tussac cover and recent change in tussac cover, on Kidney Island and (2) using these relationships, estimate the size of the breeding population on Kidney Island and on what are currently believed to be the other main breeding islands in the Falklands. To do so, we surveyed sooty shearwater burrow density and occupancy on Kidney Island, compiled similar data from previous surveys of other islands, and modeled density and occupancy as functions of habitat using HSFs and GFR models.

## 2. Materials & methods

### 2.1. Data collection, Kidney Island

We surveyed sooty shearwater burrows on Kidney Island (area = 0.32 km<sup>2</sup>; Fig. 2) from January 7 to 21, 2017. Following previous surveys of burrowing petrels on islands dominated by tussac grass (Catry et al., 2003; Lawton et al., 2006), we randomly projected a 50 × 75 m grid onto the vegetated area of the island (Fig. 2). At each grid node (n = 66), we counted the number of burrows in a circular plot of radius 2.5 m (planar area = 19.64 m<sup>2</sup>). We ignored burrows shorter than a forearm's length, as these are unlikely to be viable (Scott et al., 2008). White-chinned petrels (*Procellaria aequinoctialis*) and Magellanic penguins (*Spheniscus magellanicus*) also construct small numbers of burrows on Kidney Island (Woods, 1970) but these are wider and shallower than sooty shearwater burrows, making them easy to exclude (Parker and Rexer-Huber, 2015).

At each plot, we also recorded the following habitat indices: Aspect, soil moisture, mean tussac height, percent tussac cover, presence of bare rock, and presence of other animal species (Table A1). We hypothesized that these indices might influence burrow density or occupancy by affecting (1) shearwaters' ability to take off from the colony (e.g., distance to coast) (2) their ability to excavate burrows (e.g., soil moisture), or by (3) providing shelter from the weather or predators (e.g., tussac grass cover). We measured aspect using a magnetic compass and average tussac height (to the nearest quarter-meter) using a graduated pole. We estimated approximate percent tussac cover by eye and detected the presence of other species either directly or indirectly (e.g., over-turned or compressed tussac indicated the regular presence of South American sea lions (*Otaria flavescens*)). We classified soil moisture on an arbitrary four-point scale derived from Lawton et al. (2006): 1 (dry, well-drained), 2 (intermediate), 3 (saturated, moisture comes to the surface when pressed by hand), and 4 (standing water within the plot). In addition, we compiled two types of remotely-sensed habitat data for each plot: Firstly, we calculated distance to

**Table 1**

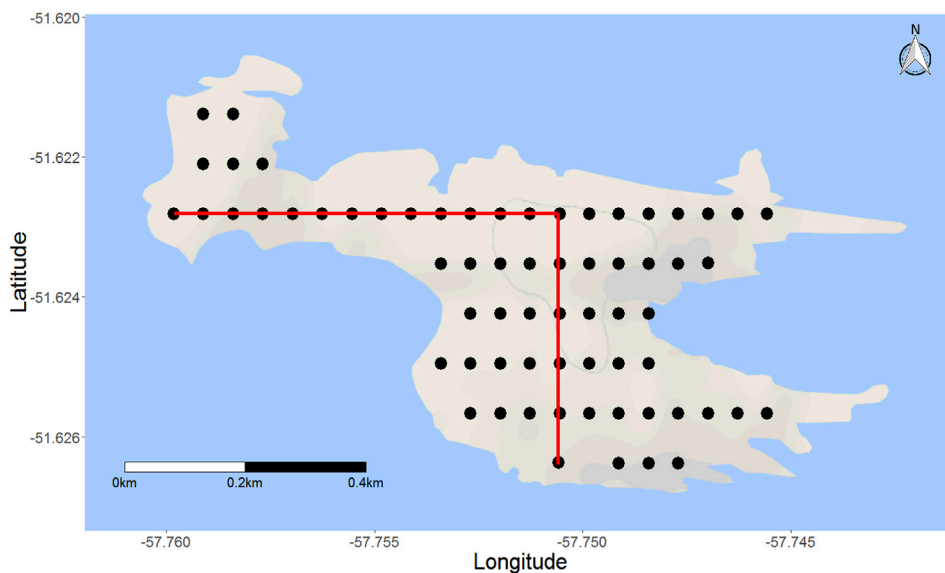
Most recent evidence of sooty shearwater breeding colonies in the Falkland Islands.

Location	Breeding Status <sup>a</sup>	Evidence								Conservation Designation <sup>f</sup>	Source
		Burrows	Eggs	Chicks	Remains <sup>b</sup>	Calls <sup>c</sup>	Odor <sup>d</sup>	Rafts <sup>e</sup>	Other		
Amy Island	L	✓					✓				Poncet et al. (2012)
Beauchene Island	P							✓		IBA, NNR	P. Catry. Pers. Comm.
Beaver Island	P								✓	IBA, IPA	Woods and Woods, 1996
Big Shag Island	L	✓					✓				Poncet and Passfield (2013)
Bird Island	L	✓			✓	✓	✓			IBA, NNR	Catry et al. (2018)
<b>Bottom Island<sup>g</sup></b>	L	✓					✓				Poncet et al. (2012)
Brandy Island	L	✓			✓		✓			IBA	Putz (2009).
Calista Island	P				✓						Poncet and Passfield (2011).
Cochon Island	P							✓	✓	IBA, NNR	S Poncet, Pers. Comm.
Flat Jason Island	L	✓			✓	✓				IBA, NNR	Woods and Woods, 1996
George Island	L	✓									Woods and Woods, 1996
<b>Ghost Island<sup>g</sup></b>	L	✓			✓					IBA	Poncet and Passfield (2012)
Grand Jason Island	P								✓	IBA	Woods and Woods, 1996
Gypsy Cove, E. Falkland	L	✓						✓	✓		McNally and Augé (2015)
Harbour Island East	L	✓									Passfield and Poncet (2010)
Harbour Island West	L	✓									Passfield and Poncet (2010)
Keppel Island	P								✓	IBA, IPA	Woods and Woods, 1996
<b>Kidney Island<sup>g</sup></b>	C	✓	✓	✓	✓	✓	✓	✓		IBA, NNR	Woods and Woods, 1996; this study
Little Motley Island	P							✓			A. Stanworth, Pers. Comm.
Motley Island	P					✓				IPA	Woods and Woods, 1996
New Island	L	✓								IBA, NNR	Strange et al. (2007)
North Fur Island	P				✓					IBA, NNR	Woods and Woods, 1996
Pebble Island	P								✓	IBA	Woods and Woods, 1996
Rum Island	L	✓								IBA	Putz (2009)
Sandy Bay Island	C	✓		✓			✓			IBA	Poncet and Passfield (2012), (N. Rendell, Pers. Comm.)
Sea Lion Island	L	✓								IBA, NNR	Woods and Woods, 1996
Sea Lion Easterly Island	L	✓			✓		✓			IBA	Putz (2009)
<b>Sophie Island</b>	L	✓					✓				Poncet et al. (2012)
Steeple Jason Island	P								✓	IBA	Woods and Woods, 1996
Stinker Island	L	✓									Passfield and Poncet (2010)
<b>Top Island<sup>g</sup></b>	L	✓					✓				Poncet et al. (2012)
Tussac Point, E. Falkland	L	✓					✓				Poncet et al. (2012)
West Point Island	P								✓	IBA	Woods and Woods, 1996
Whisky Island	L	✓			✓		✓			IBA	Putz (2009)
Wineglass Hill, E. Falkland	L	✓									Woods and Woods, 1996

Sites in **bold** are currently considered to be the main breeding colonies in the Falklands, for which we provide population estimates.<sup>a</sup> C – breeding confirmed by presence of eggs or chicks, L – breeding likely due to presence of burrows but no eggs or chicks seen, P – breeding possible due to other evidence.<sup>b</sup> Remain of adults found at the site.<sup>c</sup> Calls of adults heard at or over the site.<sup>d</sup> Odor of petrels detected by experienced observers.<sup>e</sup> Rafts of sooty shearwaters observed to form off the site in the evenings during the breeding season.<sup>f</sup> IBA = Important Bird Area; IPA = Important Plant Area; NNR = Falkland Islands National Nature Reserve.<sup>g</sup> Sites systematically surveyed during this study or by Poncet et al. (2012).

the coast and slope using the “raster” R package (Hijmans, 2016), using a digital elevation model (DEM) retrieved from the Earthdata search portal (NASA Land Processes Distributed Active Archive Centre, NASA JPL 2013). Secondly, we estimated the relative change in tussac density by comparing a satellite image captured in 2017 (Google Earth Pro, 2017) with an aerial image captured by the British Geological Survey in 1956 (Falkland Islands Department of Mineral Resources). Darker grey scale values correspond to higher tussac density, allowing us to estimate the relative change in tussac coverage from the difference in grey scale values between the 1956 and 2017 images. Small differences indicate little change in density between the years and large positive differences indicate areas of regenerated tussac.

Initial trials showed that, due to the depth and complexity of sooty shearwater burrows on Kidney Island (Clark et al., 2018), occupancy could not reliably be determined using a burrowscope (Ridgid micro CA-300 Hand-held Inspection Camera, Elyria, OH, USA). We therefore used an indirect disturbance method to record the passage of birds in or out of burrows, from which we inferred occupancy (Reyes-Arriagada et al., 2007; Parker and Rexer-Huber, 2015). We assume that a burrow is occupied if it is repeatedly visited by a breeding pair. We monitored occupancy at a subset of 18 of the 66 sampling plots aligned along two perpendicular transects spanning the major habitat gradients on the island (Fig. 2). On 10 January, we loosely erected 3–5 wooden cocktail sticks 10 cm inside the entrances to a random sample of burrows in each plot (median = 19 burrows/plot, range = 2–32). We checked each burrow every two days (5 repeat visits) and recorded any sticks that had been disturbed and re-erected them. It is possible that socializing non-breeders may have occasionally disturbed these



**Fig. 2.** Location of survey plots (black dots) on Kidney Island, Falkland Islands, and perpendicular transects used to establish the subsample of plots for occupancy sampling (red lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sticks, leading to inaccurate classification of burrow occupancy (Scott et al., 2009; Parker and Rexer-Huber, 2015). However, we assumed that repeated entrance/exit over 10 days in the chick-rearing period (during which breeders enter their burrows every 1–2 nights; Hedde et al., 2014) was indicative of breeding.

## 2.2. Data from other breeding sites

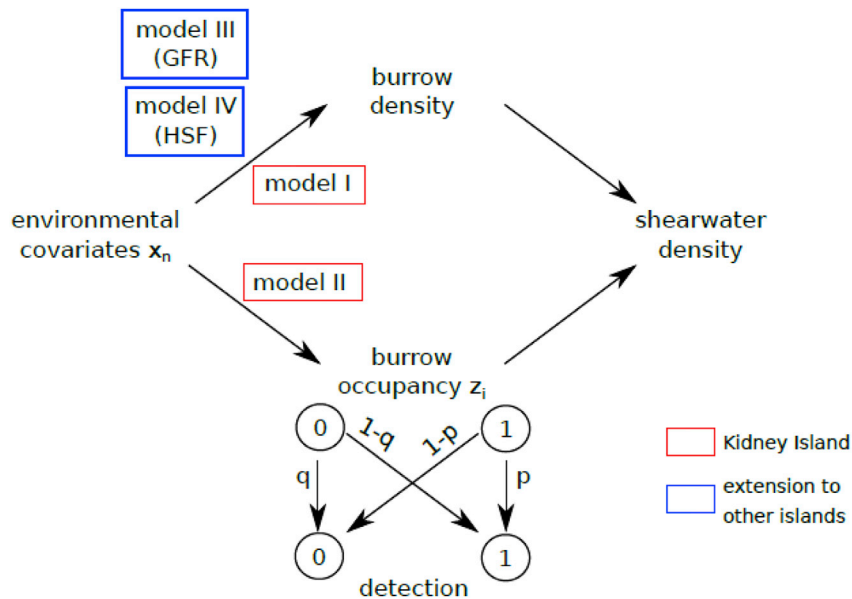
The known distribution of shearwaters in the Falkland Islands was summarized by Woods and Woods (1996), largely based on reports received from members of the public. Since then many other breeding locations have been discovered. We compiled reports of breeding sites in the archipelago from our own observations, the South Atlantic Environmental Research Institute, Falklands Conservation, the Falkland Islands Government, local observers and Woods and Woods (1996), in order to map the current known distribution of sooty shearwaters in the Falkland Islands (Fig. 1; Table 1). In order to estimate the numbers of sooty shearwaters potentially breeding at what are presumed to be the five largest known colonies in the Falklands Islands other than Kidney island (Top, Bottom, Amy, Sophie, and Ghost Islands), we compiled data from previous surveys (Fig. 1; Table 1). Like Kidney Island, these are small islands, densely covered in tussock grass. However, all had introduced rodents that may have suppressed sooty shearwater breeding numbers, until they were eradicated between 2001 and 2011. Systematic surveys of sooty shearwater burrows have been carried out at two islands, Top and Bottom (Poncet et al., 2012). Burrow density was surveyed on these islands using strip transects of length 20–100 m. Occupancy was confirmed by visual inspection and audio playback of taped sooty shearwater calls but the rate of occupancy was not estimated (Poncet et al., 2012). No systematic survey data were available for the other islands, so we used a habitat model-based approach to estimate population sizes there (see below).

## 2.3. Statistical analysis

Unless otherwise stated, we carried out all analysis in R (R Core Team, 2013). To allow effect sizes to be compared on a common scale, we standardized explanatory covariates prior to model fitting. We modeled burrow density on Kidney Island as a function of habitat (Model 1; Fig. 3) using generalized linear models (GLMs) with Poisson errors and a log link function. Starting with a model containing all candidate explanatory variables and their biologically plausible interactions (Table A1), we simplified models using backwards selection until we minimized the AIC (Burnham and Anderson, 2003). We assumed that conspecific attraction would manifest as spatial autocorrelation. To model this, we also considered a “neighborhood” auto-covariate (Augustin et al., 1996), calculated for each plot by averaging burrow density in the four nearest plots. To test for residual spatial autocorrelation, we calculated Moran's I at 80 m, the average distance between plots. For consistency with information-based model selection, we quote mean effect sizes and their 85% confidence intervals (Arnold, 2010).

We modeled occupancy as a function of habitat and burrow density (Fig. 3) using a hierarchical Bayesian model fitted in JAGS, via R (Plummer, 2016). To account for the fact that occupancy detection via the disturbance method was imperfect, we modeled the probability both of correctly and incorrectly detecting occupancy at each burrow (see Supplementary Materials for details; Fig. 3). We built a minimum adequate model (Model II) using forwards stepwise model selection by adding





**Fig. 3.** Relationships between models used to estimate population size in this study. Models I and II predict, respectively, burrow density and occupancy on Kidney Island as functions of habitat. Detection uncertainty is defined in Model II by:  $p$ , the probability of correctly detecting burrow occupancy;  $q$ , the probability of correctly detecting burrow vacancy;  $1-q$ , the probability of recording a burrow as occupied when it is not; and  $1-p$ , the probability of recording a burrow as vacant when it is occupied. Models III and IV predict burrow density as functions of habitat in what are currently believed to be the main sooty shearwater colonies in the Falklands, other than Kidney Island, not all of which have been surveyed. Model III includes Generalized Functional Response terms to account for variation in habitat selection due to differing habitat availability among islands. Model IV is a conventional Habitat Selection Function.

plausible candidate explanatory variables (Table A1) if they resulted in a reduction in the deviance information criterion (DIC) (Spiegelhalter et al., 2002). To examine the spatial distribution of regions of high burrow density but low occupancy (and vice versa), we standardized gridded burrow occupancy and density, and subtracted the former from the latter.

We estimated the breeding population of sooty shearwaters on Kidney Island, together with its associated uncertainty, using a parametric bootstrapping technique. For each cell on the survey grid, we predicted burrow density and occupancy using parameter values drawn randomly from the multivariate normal distribution associated with Model I and the posterior distributions associated with Model II. We then integrated the product of density and occupancy across the survey grid to arrive at an estimate of the number of breeding pairs on the island. We repeated this procedure 1,000 times and calculated the mean and its associated 95% confidence intervals. Ideally, occupancy is assessed just after the laying period (11–24 November on Kidney Island; Hedd et al., 2014). We were constrained to carry out fieldwork around the beginning of the hatching period (11 January – 1 February), by which time a small but unknown proportion of breeding attempts may have failed. Hence, we regard this as a minimum population estimate.

To predict burrow density on other islands, we fitted a Generalized Functional Response (GFR) habitat selection model (Model III; see Supplementary Materials) to observed burrow densities on Kidney, Top, and Bottom Islands using the R package “HATOPO” (available from JM). GFRs are extensions of traditional HSFs that allow model coefficients to vary with regional habitat availability (Matthiopoulos et al., 2011). We specified Poisson errors with a log-link function, and plot area as an offset. Habitat data for the other islands was limited to DEM-derived covariates (aspect, slope, elevation, and distance to coast). Additionally, we considered the historical presence (i.e., prior to 2009) of introduced rodents as a categorical explanatory covariate. The starting model of burrow density contained all candidate explanatory variables, their biologically plausible interactions, and their second-order regional expectations (Matthiopoulos et al., 2011), where region was defined as an island. We reduced this model by backwards selection until we reached the lowest AIC (Burnham and Anderson, 2003). After model selection, we modeled conspecific attraction as described above, with the exception that burrow density was averaged across the nearest 2 transects and Moran’s  $I$  was calculated at 72 m, the average distance between transects. We also fitted a conventional HSF model (Model IV), which was equal to Model III, minus the GFR terms, and tested whether this predicted density as well as the more complex GFR model (Model III).

To estimate the number of occupied burrows on both the surveyed islands (Kidney, Top and Bottom) and those with no systematic survey data (Ghost and Amy) we first predicted burrow density on grids covering these island using both Models III and IV (i.e., using HSF and GFR models). We then multiplied these grids by the mean occupancy rate on Kidney Island predicted by Model II (no other data were available for the other islands) and integrated across each. For comparison, we also calculated design-based estimates of the number of burrows on Kidney, Top and Bottom Islands by multiplying the mean observed density on each island by the extent of their vegetated areas (Rayner et al., 2007a). We converted these to estimates of the number of occupied burrows by multiplying by the mean observed occupancy rate on Kidney Island.

### 3. Results

#### 3.1. Habitat selection and population size, Kidney Island

Observed mean burrow density on Kidney Island was  $0.60 \pm 0.06$  burrows/m<sup>2</sup> (range 0–1.73 burrows/m<sup>2</sup>,  $n = 66$ ). The neighborhood covariate improved model fit and removed residual spatial autocorrelation from Model I (Moran's  $I = -0.063$ ,  $p = 0.327$ ; AIC = 420.9; pseudo  $R^2 = 70.87\%$  vs. model without this covariate, Moran's  $I = 0.081$ ,  $p = 0.049$ ; AIC = 460; pseudo  $R^2 = 56.47\%$ ). Model I suggests a positive relationship between burrow density and slope, elevation, tussac cover, and change in tussac density; and a negative relationship with distance from the coast (Table 2). Tussac cover and tussac height interacted synergistically to result in a decreased burrow density (Table 2; Fig. A1). Aspect and tussac height and interactions between distance to coast and elevation, and slope and elevation, were also retained in Model I, but had only slight and non-significant effects (Table 2). Ranks of Akaike weights support the relative importance of these terms (Table A2). Predicted burrow density on Kidney Island averaged 0.588 (95% CRI = 0.466 to 0.709) and was highest in coastal regions, especially at the western end of the island (Fig. 4A).

Model II suggests positive relationships between burrow occupancy on Kidney island and elevation and change in tussac density, and a negative relationship with distance to the coast (Table 3). Slope was retained in Model II, but had only a slight and non-significant effect. Burrow density was not retained. Ranks of Akaike weights support the relative importance of these terms (Table A3). Predicted burrow occupancy was very high (~100%) in all coastal regions and at the western end of Kidney Island but almost zero in some inland areas (Fig. 4B). Together, Models I and II predict that 139,674 (95% CI = 90,263 to 208,121) burrows were occupied on Kidney Island during our study (Fig. 4C). High burrow density but low occupancy was predicted in western end of the island, especially in steep areas (Fig. 4D). Conversely, low density and high occupancy was predicted in the northeast and in some coastal regions.

#### 3.2. Population size, other islands

Model III (the GFR model) predicted that Top, Bottom, Amy, Sophie, and Ghost Islands hold 43,087 burrows (95% CI = 34,184–51,871; Table 4). Assuming for the sake of expediency that they have the same occupancy rate as Kidney Island, this would equate to 25,335 occupied burrows (95% CI = 20,079–30,549). In contrast, Model IV (the conventional HSF model) predicted a total of 264,578 burrows on these islands (95% CI = 209,682–319,023), which equates to 155,572 occupied burrows (95% CI = 123,293–187,586). Using Models I and III, we estimated there to be 214,079 sooty shearwater burrows in the Falklands, occupied by 165,009 breeding pairs (95% CI = 110,342–238,669). For comparison, the equivalent design-based estimate, assuming a mean occupancy rate equal to that observed on Kidney Island, would be ~132,582 breeding pairs (95% CI = ~12,189–~188,621). Altogether, our review of available data showed evidence of sooty shearwater presence at 28 additional islands in the Falklands archipelago but breeding was either confirmed or probable at only 15 of these (Fig. 1). There were insufficient data to predict population size at these additional unsurveyed islands.

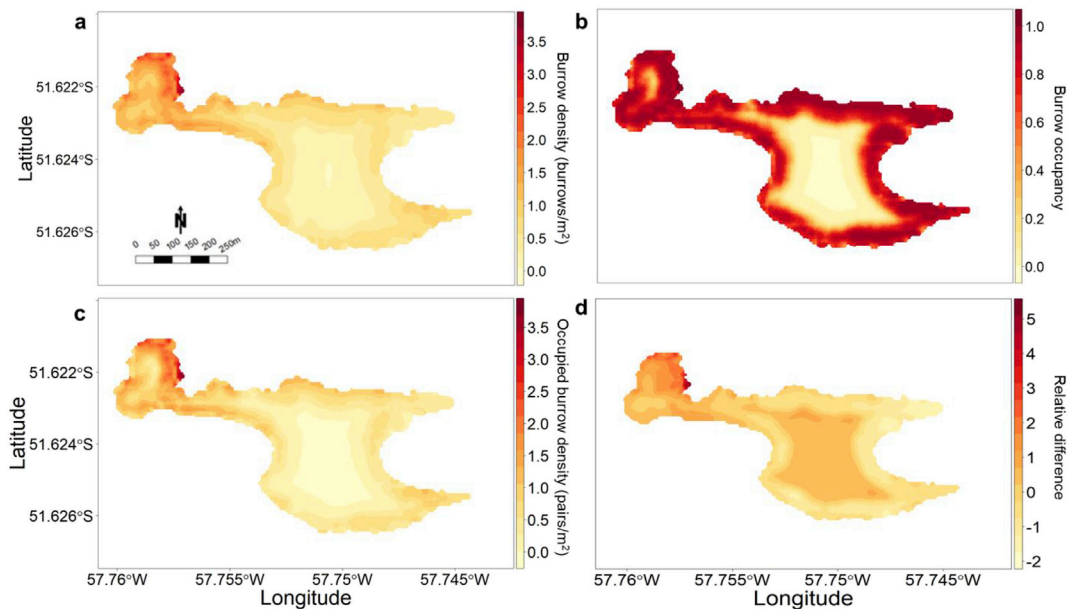
Model III predicted sooty shearwater burrow density on other known breeding islands better than Model IV (likelihood ratio test:  $\chi^2 = 99.335$ ,  $p < 0.0001$ ; AIC = 848.2 vs. 1046; pseudo  $R^2 = 70.0\%$  vs. 54.9%; Fig. A2). Inclusion of the neighborhood covariate improved model fit in both models and reduced residual spatial autocorrelation to negligible levels in Model III (for Model III and Model IV with the covariate: Moran's  $I = -0.006$  and 0.103,  $p = 0.426$  and 0.009 vs. Moran's  $I = 0.139$  and without the covariate: 0.254,  $p = 0.009$  and 0.010; AIC = 952.1 and 1258).

### 4. Discussion

Model selection showed that models containing habitat covariates explained burrow density and occupancy better than the equivalent intercept-only models. Population sizes predicted using the latter are equivalent to design-based estimates (i.e., mean burrow density x mean occupancy x area). By modeling sooty shearwaters' habitat selection and occupancy, we were therefore able to estimate the size of their colony on Kidney Island in the Falkland Islands with greater accuracy than would have been possible using the conventional design-based estimation techniques. The width of the 95% CI for the habitat

**Table 2**  
Standardized parameters estimated by Model I of sooty shearwater burrow density on Kidney Island as a function of habitat.

Parameter	Estimate	85% Confidence Interval
Aspect	−0.038	−0.147, 0.071
Distance to coast	−0.261	−0.442, −0.081
Elevation	0.192	0.016, 0.369
Slope	0.260	0.091, 0.429
Distance x Elevation	0.001	−0.183, 0.186
Slope x Elevation	0.059	−0.111, 0.229
Change in tussac density	0.121	−0.003, 0.246
Tussac cover	0.148	0.014, 0.282
Tussac height	0.009	−0.119, 0.138
Tussac cover x Tussac height	−0.115	−0.214, −0.016



**Fig. 4.** Predicted distribution of breeding sooty shearwaters on Kidney Island, showing, (a) burrow density; (b) burrow occupancy; (c) occupied burrow density; and (d) the relative difference between burrow density and occupancy. Positive differences indicate areas of high burrow density and low occupancy, whereas negative differences indicate areas of low burrow density and high occupancy.

**Table 3**

Standardized parameters estimated by Model II of sooty shearwater burrow occupancy on Kidney Island as a function of habitat.

Parameter	Estimate	85% Confidence Interval
Slope	−0.823	−1.640, 0.079
Distance to coast	−5.041	−7.697, −2.245
Elevation	2.102	0.589, 3.492
Change in tussac density	1.031	0.268, 1.773

**Table 4**

Estimated sizes of sooty shearwater breeding populations at what are currently thought to be the main colonies in the Falkland Islands.

Island	Burrows		Occupied burrows		
	Design-based <sup>a</sup>	Model I or III	Design-based <sup>b</sup>	Model I or III	Model IV
Kidney	152,760	170,992	115,792	139,674	—
Top	17,400	20,720	13,189	12,183	4,314
Bottom	3,750	10,765	2,843	6,330	135,641
Amy	<800 <sup>c</sup>	10,147	<606	5,966	53,049
Sophie	<200 <sup>c</sup>	166	<152	98	13,102
Ghost	NA	1289	NA	758	58,472
Total	174,910	214,079	132,582	165,009	—

<sup>a</sup> Mean observed burrow density x extent of the vegetated area.

<sup>b</sup> Mean observed burrow density x extent of the vegetated area x mean occupancy.

<sup>c</sup> Estimated by Poncet et al. (2012).

model-based estimate was 117,858 occupied burrows, whereas that for the intercept-only model-based estimate would have been 176,491 occupied burrows. We therefore conclude that habitat model-based estimates of population size are more accurate than design-based estimates. Our results confirm that this colony is now at least two orders of magnitude larger than it was in the 1950s. Both burrow density and occupancy were positively dependent on the estimated change in tussac density between 1956 and 2017. That is, colony growth has occurred in areas where tussac has regenerated following the cessation of harvesting. This indicates that breeding habitat restoration may help to reverse population declines in the Falklands and other parts of the species' breeding range. We also modeled survey data from three other colonies using Generalized Functional Response (GFR) models. Although the efficacy of this method was limited by scant survey data currently available for sooty shearwaters in the Falklands, it allowed us to provide first population estimates for these and several other poorly studied colonies in the region.



#### 4.1. Habitat selection, Kidney Island

We found that topography on Kidney Island had a large effect on burrow density and occupancy. It has been suggested that sooty shearwaters breed in areas with high slopes and elevations because these provide better drainage, reducing the risk of flooding or collapse of burrows (Stokes and Boersma, 1991; Rayner et al., 2007a), and large scale geo-morphological features (e.g., cliffs, high points on islands) might serve as aids in nest location (Brandt et al., 1995; Scott et al., 2009). Furthermore, nesting on higher slopes may allow easier takeoff because wind speeds tend to be higher in such areas (Warham, 1990; Scott et al., 2009; Whitehead et al., 2014). This may be particularly important to sooty shearwaters, as they have one of the highest wing loadings of the *Procellariidae* family (Warham, 1977). Burrow density and occupancy was negatively related to distance to the coast, possibly because there are more obstacles (e.g., dense tussac) to navigate through prior to take-off as distance to the coast increases (Oka et al., 1996; Charleton et al., 2009). We noted that sometimes, when birds failed to take off properly when leaving the colony, they would walk to the water's edge, swim out some distance, and then take off from the sea. Nesting close to the coast may therefore reduce the cost of failed take-offs.

Other covariates that affected burrow density and occupancy on Kidney Island included tussac cover, tussac height, and change in tussac density. Vegetation has been found to influence the density of burrows of Cook's petrels (*Pterodroma cookii*) (Rayner et al., 2007a) and spectacled petrels (*Procellaria conspicillata*) (Ryan et al., 2006). Denser tussac cover may improve habitat quality for breeding sooty shearwaters by offering protection from climatic extremes or by leading to the development of more favorable substrate for excavation (Stokes and Boersma, 1991; Scott et al., 2009; Clark et al., 2018). The interaction term between tussac cover and height suggests that when tussac is short, burrow density increases with the proportion of ground covered with tussac (Fig. A1), possibly because greater tussac cover provides better nest protection in those conditions. Conversely, when tussac is tall, burrow density decreases with the proportion of ground covered with tussac (Fig. A1). This is perhaps because the advantages of nest protection are eventually outweighed by the barrier that vegetation causes to takeoff or because denser vegetation makes it harder for shearwaters to find their burrows when returning from foraging trips. We assume that the positive relationship between burrow density (and occupancy) and the difference in aerial image grey scale between 1956 and 2017 occurs because this is a proxy for areas of tussac regeneration.

The performance of Model I improved and residual spatial autocorrelation decreased with the addition of the neighborhood covariate, which represented conspecific attraction between shearwaters. It is possible that residual spatial autocorrelation was present in Model I prior to the addition of this covariate because an important habitat covariate was missing. However, we considered all covariates suggested by the literature. We conclude therefore that inclusion of the neighborhood covariate supports the hypothesis that recruiting sooty shearwaters trade off the costs of nesting in potentially suboptimal habitat at the margins of colonies against the benefits of colonial breeding. In such situations, design-based survey methods will tend to overestimate population size because it will be assumed that all suitable habitat is occupied.

We found that burrow occupancy on Kidney Island averaged 0.588, which is within the range observed at other breeding sites (0.23–0.74) (Warham and Wilson, 1982; Jones et al., 2003). The probability of correctly detecting occupancy was 0.934, whereas correctly detecting non-occupancy was 0.697. These figures are similar to those found in studies that used burrowscopes to estimate occupancy by burrowing petrels (McKechnie et al., 2007; Waugh et al., 2013; Whitehead et al., 2014). Occupancy measurements can be greatly affected by the time period in which the birds are surveyed (Parker and Rexer-Huber, 2015). The ideal time to carry out burrowing petrel breeding surveys is early in the breeding season, where few burrows are likely to be visited by non-breeders and abandonment due to breeding failure is minimal (Schumann et al., 2013; Parker and Rexer-Huber, 2015). While we aimed to carry out our survey as early as possible in the breeding season, we were constrained by tracking work being undertaken at the same time to collect data during the late incubation/early hatching period. It is possible that some shearwaters had already abandoned breeding attempts by this time, which would result in an underestimation of the breeding population size (Parker and Rexer-Huber, 2015). On the other hand, socializing non-breeders attend colonies in increasing numbers as the breeding season progresses, possibly resulting in an inflation of our occupancy estimates. Future work could refine our population estimate by assessing occupancy early in the breeding season, ideally just after the main laying period (Parker and Rexer-Huber, 2015), which on Kidney Island is the 22nd of November (range = 17th – 24th of November; Hedd et al., 2014).

#### 4.2. Population size, Kidney Island

We estimate there to have been 140,000 occupied burrows on Kidney Island during the survey period. This is much higher than previous population estimates (Table 5), and supports the supposition based on periodic informal estimates that the Kidney Island population has grown rapidly since tussac-cutting on the island ceased in the 1950's. Previous estimates of the size of the Kidney Island population were made simply by estimating burrow density in a small area and multiplying this by a rough estimate of the extent of suitable habitat (R.W. Woods, pers. comm.). As discussed above, this may have led to an overestimate. Nonetheless, the estimates were made by highly competent observers and are probably accurate to an order of magnitude. Hence, the Kidney Island colony has grown by at least two orders of magnitude in the past half century, an annual growth rate of around 7% (Table 5). This is a rapid but plausible rate, similar to those observed in northern fulmars (*Fulmarus glacialis*) and northern gannets (*Sula bassanus*) in the Northeast Atlantic in the 20th century (Nelson, 1965; Cramp et al., 1974; Jones, 2002). It is unclear if growth of the Kidney Island colony has been purely due to local production or whether immigration has contributed. Natal and adult breeding philopatry are high among *Procellariiformes* (Warham, 1990; Brooke, 2004).

**Table 5**

Estimated numbers of sooty shearwaters breeding on Kidney Island, Falkland Islands and putative annual percent growth rate.

Occupied Burrows	Year	Reference	Annual Growth Rate <sup>a</sup>
2,000	~1960	Woods (1970)	—
10,000–20,000	1996	Woods and Woods, 1996	11.1–25%
100,000	2006	Woods and Woods (2006)	40–90%
139,674	2017	This study	3.6%

<sup>a</sup> Between consecutive estimation periods.

Nonetheless, immature sooty shearwaters could recruit to Kidney Island from elsewhere. For example, there are thought to be extensive colonies on islands and fjord coastlines of Patagonia and Tierra del Fuego, although little is known about their population size, trends, or conservation status (Lawton et al., 2006; Reyes-Arriagada et al., 2007). If some fledglings from these colonies disperse into the North Atlantic, they would pass the Falklands and might therefore be likely to recruit to Kidney Island. A tracking or large-scale mark-recapture study would be required to establish if this were the case.

Single population surveys do not count adults that skip breeding in the survey year (Warham, 1990; Newman et al., 2008). It has been estimated that between one-fifth and one-half of breeding petrels miss breeding in any one year (Brooke, 2004). Based on these figures, our figures would equate to a population at Kidney Island of 168,000 to 280,000 breeding pairs of sooty shearwaters at Kidney Island. Furthermore, we assumed that only one breeding pair occupied a burrow and consequently, population size may be underestimated. This is because burrows can be interconnected and shared between conspecifics (Hamilton, 2000). As far as practicable, we modeled detection error caused by false positives (e.g., prospecting breeders, weather, or vegetation knocking over sticks) and false negatives (e.g., birds escaping via another tunnel, thereby not knocking over sticks). Accounting for this error, as well as spatial variation in occupancy rates, should have improved the accuracy of our population estimates compared to other studies.

#### 4.3. Population size and distribution, other islands

We estimated that approximately 25,000 burrows are occupied by sooty shearwaters in what current evidence suggests are the main colonies in the Falkland Islands other than Kidney Island, representing over one-seventh of the total for the archipelago (Table 4). The number of sites where sooty shearwaters are known or suspected to breed in the Falklands has increased from 6 to 21 in the past twenty years. Almost all are located on rodent-free, tussac-covered offshore islands, with most on the east and south coasts of the Falklands archipelago (Fig. 1; Woods and Woods, 1996). This trend may indicate that new breeding sites are being established in the Falklands, perhaps due to the growth evident at Kidney Island. However, this could also be an artefact of the increased effort devoted to exploring the avifauna of the Falklands in recent years (Table 1). Some islands not included in our population estimate may hold large numbers of breeding sooty shearwaters. For example, sooty shearwaters are suspected to breed on Cochon Island (0.04 km<sup>2</sup>), which is only 2.5 km from Kidney Island, but this has not been confirmed due to the difficulty of landing there. Similarly, it remains possible that there are substantial sooty shearwater colonies in the archipelago yet to be discovered so we cannot provide an overall population estimate for the archipelago.

Predictions from Model III (the GFR) to unobserved islands were realistic in some cases but unrealistic in others. This, we suspect, may result from two separate factors. First, the predictions may be extrapolations not interpolations in environmental availability space. To provide better predictions it would have been necessary to sample across the spectrum of availability. Predictions for Top, Bottom, and Amy Islands were all higher than survey data suggest, possibly because these populations were more recently established and released from ecological pressures of rodents than on Kidney Island. Recently, Top, Bottom, Ghost, and Amy Island had rodents eliminated and there is evidence of a rapid increase in burrows along the coasts of Bottom Island (Poncet et al., 2012). Therefore, predictions from Model III may be better thought of as population sizes likely to be attained on these islands if growth follows the pattern on Kidney Island. The second factor that may cause unrealistic results for some islands was that we did not have occupancy data for them. As a first approximation, we estimated their population sizes by assuming that mean occupancy on those islands was the same as on Kidney Island. However, as we have shown, occupancy on Kidney Island was partially dependent on habitat so this assumption may be wrong. Our results for the other islands should therefore be treated with caution. Another approach would have been to use Model II, which we fitted to occupancy data from Kidney Island, to predict occupancy on the other islands as a function of their habitats. However, without occupancy data from the other islands, we could not account for any functional responses of occupancy to inter-island differences in habitat availability. In future studies it would be valuable to test whether such functional responses occur by surveying both occupancy and habitat at multiple sites.

Traditional techniques of estimating population size, such as the design-based method of multiplying burrow density by observed breeding habitat and simple HSFs may misrepresent the total breeding population size. We found that the design-based method underestimated population size by over 20% across the Falklands when compared with habitat-based results in Models I and III (Table 4). A critical assumption of design-based techniques is that burrow densities from surveyed areas reflect densities in un-surveyed areas. However, as observations from surveys are averaged across space, areas of local extremes may be lost. Furthermore, as our study and past studies have demonstrated, seabird burrowing density and occupancy

rely heavily on breeding micro-habitat (Rayner, Hauber & Clout, 2007b). Thus, utilizing a spatial, model-based approach may capture the effect of these “hot or cold spots” on population estimates, allowing for a more precise approximation of population size. Previous studies of seabirds have shown that design-based procedures often estimate population size poorly (e.g., Rayner et al. 2007; in contrast, see Scott et al., 2009) compared to model-based methods. Our study supports this result and moreover shows that because occupancy too varies as a function of habitat that assuming a uniform occupancy rate across space will reduce the accuracy of population estimates.

We used GFRs (Model III) to estimate burrow densities and potential population size for a number of islands using a limited dataset. This modeling technique is useful for areas like the Falklands, where there are a lot of islands and limited resources available to survey animal populations (Otley et al., 2008). Despite limited survey data from other islands and a small number of explanatory covariates, we found that Model III (the GFR model) fit much more robustly than Model IV (the conventional HSF model) fitted to burrow observations. This indicates that the form of the functional response of sooty shearwaters to breeding habitat varies with local habitat availability. As such, a habitat selection model fitted to data from one island will not necessarily predict burrow density well at another island unless a GFR model is used (Matthiopoulos et al., 2011).

#### 4.4. Conservation and management implications

Our results support the supposition that the breeding population of sooty shearwaters in the Falkland Islands (South Atlantic) is increasing, which contrasts with declining populations in the species' core breeding range in the South Pacific. It is thought that breeding habitat loss has been one contributory cause of sooty shearwater declines in New Zealand (Jones, 2000; McKechnie et al., 2008). Tussac harvesting and fire drastically reduced tussac cover, height, and age on Kidney Island prior to the 1950s so breeding habitat loss could formerly have limited population size in the Falkland Islands and tussac regeneration following the cessation of these activities facilitated its recent increase. However, there are several other rodent-free, tussac covered islands in the Falklands, on which it appears that sooty shearwaters could have bred in the recent past but did not. This raises the question of whether breeding habitat availability was really limiting in the past. In answer, we note that petrels have a strong propensity to recruit to existing colonies, rather than founding new ones (Warham, 1996). This may be because immature birds tend to locate colonies by following or detecting conspecifics. If so, then new colonies are more likely to be founded near old ones. Our results are consistent with this: Rodents were eradicated from the tussac-covered Top and Bottom Islands, which are only 6 km from Kidney Island, in 2001, since then they appear to be being rapidly colonized by sooty shearwaters. In contrast, a recent thorough survey of Bird Island, 230 km away on the other side of the Falklands archipelago, which has always been tussac covered and rodent-free, found no confirmed breeding sooty shearwaters (Catry et al., 2018). As such, there could be a large temporal lag between the loss of breeding habitat at one colony and the establishment of new colonies at alternative but distant locations. If this is so, breeding habitat restoration and the removal of invasive predators should initially be targeted at or near existing or traditional breeding sites. Ongoing habitat restoration projects in other parts of the Falklands and elsewhere should therefore be regarded as long-term enterprises.

Of course, other factors may also have formerly limited the size of the Falkland Islands sooty shearwater population. For example, it may have been impacted by fisheries in the North Atlantic, such as the now defunct Grand Banks cod fishery (Uhlmann, 2003), which occurred within the core wintering range of sooty shearwaters from the Falkland Islands (Hedd et al., 2012). Indeed, until relatively recently great shearwaters (*Puffinus gravis*) were caught in large numbers on baited hooks for use as bait in this fishery (Bent, 1964). It seems likely that many sooty shearwaters would have been caught at the same time. Sooty shearwaters were also bycaught in large numbers in gillnets in the Northwest Atlantic (Uhlmann et al., 2005; Benjamins et al., 2008) but it is unclear whether bycatch has reduced sufficiently since the 1950s to account for the increased population in the Falkland Islands.

Ultimately, the apparently opposite breeding population trajectories of sooty shearwaters in and around New Zealand and the Falklands could be caused by multiple interacting effects. Firstly, bycatch rates may differ between waters around New Zealand and those around the Falklands (Uhlmann et al., 2005; Auge and Golding, 2017) or between the North Pacific and Northwest Atlantic where the respective populations winter (Shaffer et al., 2006; Hedd et al., 2012). Secondly, winter survival could vary between the two populations due to differential effects of climate change on wind patterns, productivity, etc. (Shaffer et al., 2006; Hazen et al., 2012), but very little is known about this at present. More tangibly, invasive rodents have been eradicated from or were never present on sooty shearwaters breeding islands in the Falklands (Table 1; Tabak et al., 2014). In contrast, most colonies in New Zealand still harbour rat populations (Newman et al., 2008, 2010). Finally sooty shearwater chicks and fledglings are harvested by indigenous Maori in New Zealand (Lyver, 2000; Newman et al., 2010), while there is no equivalent harvest in the Falklands. Ultimately, comparative studies on the demography and movements of the two populations may be needed if the reasons for their very different conservation prospects are to be understood.

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## Appendix A

**Table A1**

Summary of covariates considered in Models I and II. Covariates in bold were included in the minimum adequate model of burrow density (Model I) and underlined variables were included in the minimum adequate model of burrow occupancy (Model II).

Effects	Effect on sooty shearwater burrows/occupancy
<b>Aspect</b>	Facilitates take-off
<b>Slope</b>	Facilitates take-off; higher surface area in plots with higher slope
<u>Distance to Coast</u>	Facilitates take-off
<u>Elevation</u>	Facilitates take-off
Soil Moisture	Facilitates easier construction of burrows
<b>Tussac Cover</b>	Improves drainage; protection from weather; easier construction; etc.
<b>Tussac Height</b>	Protection from weather; easier construction of burrows
<u>Change in Tussac Density</u>	Facilitates easier construction of burrows
Rock Presence	Impedes construction of burrows
<b>Tussac Cover x Tussac Height</b>	Improves drainage; protection from weather; easier construction; etc.
Tussac Cover x Tussac Age	Improves drainage; protection from weather; easier construction; etc.
<b>Distance to Coast x Elevation</b>	Facilitates take-off
<b>Slope x Elevation</b>	Facilitates take-off
Slope x Distance to Coast	Facilitates take-off

**Table A2**

Summary of the selection of Model I. Due to the large number of possible models in the selection process, models below are defined by deletion of main effects (and all pertinent interactions) from the minimum adequate model. Models are ranked by  $\Delta AIC$ .

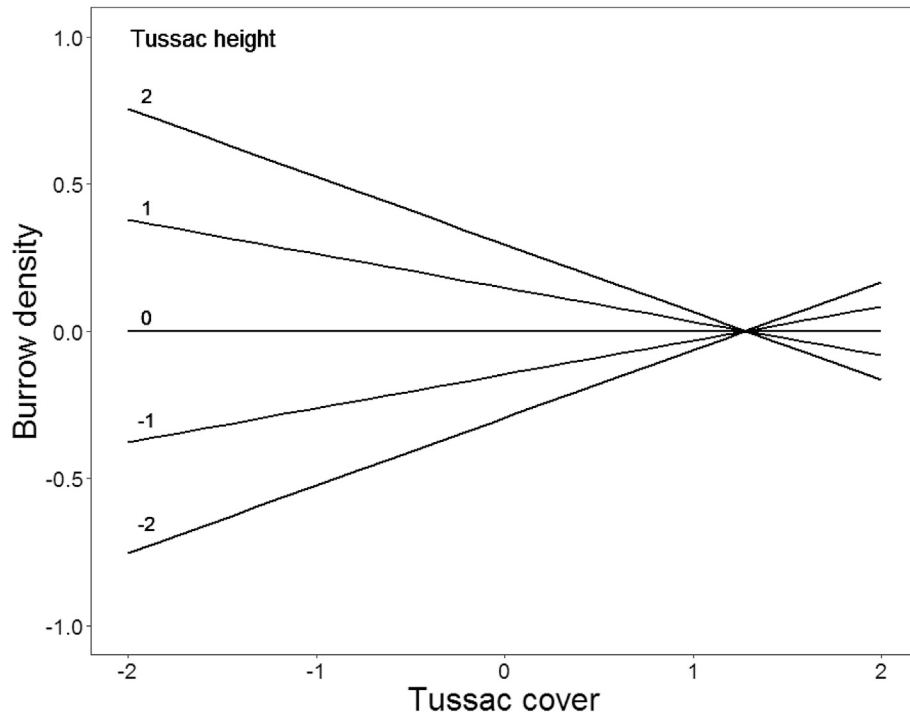
Model	Number of parameters	$\Delta AIC$
Minimum Adequate	12	0.000
- aspect	11	2.540
- slope	10	6.700
- tussac height	10	10.060
- tussac cover	10	33.770
- change in tussac density	11	38.480
- elevation	9	53.690
- distance to coast	10	94.310
Intercept only	1	325.270

**Table A3**

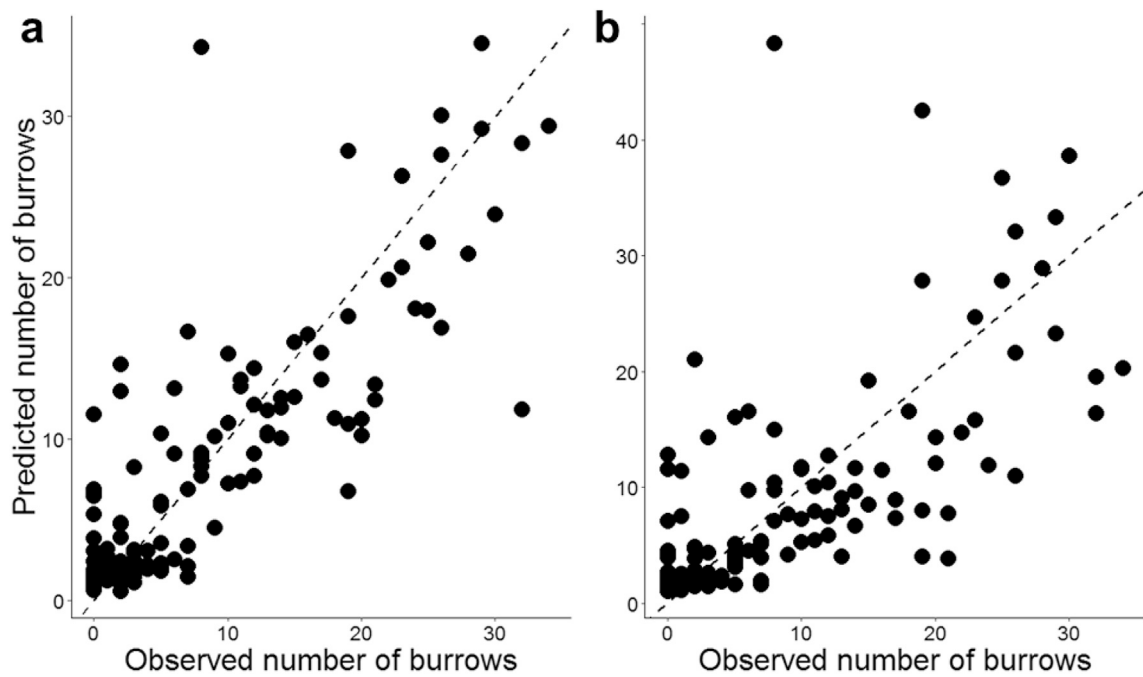
Summary of the selection of Model II. Models are ranked by  $\Delta DIC$ . See Table 2 for full list of candidate variables.

Model	Effective number of parameters*	$\Delta DIC$
Minimum Adequate	21.713	0.000
DC + EL + SL	21.184	1.895
DC + EL	21.994	2.870
DC	24.314	6.527
Null	29.891	12.106
Full	28.222	15.708

\*Estimated following Spiegelhalter et al., (2002). DC = distance to the coast; EL = elevation; SL = slope; Null = only intercept term included; Full = all candidate variables and interactions included.



**Fig. A1.** The effect of tussac height and cover on burrow density predicted by Model I.



**Fig. A2.** Observed vs. predicted burrow counts for (a) Model III and (b) Model IV. Each dot corresponds to survey plots on Kidney Island, Top Island, or Bottom Island. The dashed line has a gradient of one.

## Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00554>.



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