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The impacts of introduced House Mice on the breeding success of nesting seabirds on Gough Island

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Invasive species are the main threat to island biodiversity; seabirds are particularly vulnerable and are one of the most threatened groups of birds. Gough Island, a UNESCO World Heritage Site in the South Atlantic Ocean, is an Important Bird and Biodiversity Area, and one of the most important seabird colonies globally. Invasive House Mice *Mus musculus* depredate eggs and chicks of most seabird species on the island, but the extent of their impact has not been quantified. We used field data and bootstrapped normal distributions to estimate breeding success and the number of surviving chicks for 10 seabird species on Gough Island, and compared estimates with those of analogous species from predator-free islands. We examined the effects of season and nest-site location on the breeding success of populations on Gough Island, predicting that the breeding success of Gough birds would be lower than that of analogues, particularly among small burrow-nesting species. We also predicted that winter-breeding species would exhibit lower breeding success than summer-breeding species, because mice have fewer alternative food sources in winter; and below-ground nesters would have lower breeding success than surface nesters, as below-ground species are smaller so their chicks are easier prey for mice. We did indeed find that seabirds on Gough Island had low breeding success compared with analogues, losing an estimated 1 739 000 (1 467 000–2 116 000) eggs/chicks annually. Seven of the 10 focal species on Gough Island had particularly high chick mortality and may have been subject to intense mouse predation. Below-ground and winter breeders had lower breeding success than surface- and summer-breeders. MacGillivray's Prion *Pachyptila macgillivrayi*, Atlantic Petrel *Pterodroma incerta* and Tristan Albatross *Diomedea dabbenena* are endemic or near-endemic to Gough Island and are likely to be driven to extinction if invasive mice are not removed.

Keywords: invasive species, island restoration, population ecology, rodents, seabird conservation.

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Biological invasions are among the greatest threats to native biodiversity (Clavero & Garciaberthou 2005, Bellard *et al.* 2016). The impact of invasive species is often felt disproportionately on oceanic islands (Tershy *et al.* 2015), where native biodiversity is lower (Lodge 1993), ecological competitors may be absent (Lister 1976) and/or species have evolved in the absence of terrestrial predators and, hence, are ill-equipped to defend themselves effectively (Moors & Atkinson 1984, Diamond 1989, Blumstein & Daniel 2005). This is particularly true of birds (Duncan & Blackburn 2007, Clavero *et al.* 2009); of more than 150 bird species to have gone extinct since 1500, a large proportion were island endemics (Hume, 2017). Moreover, many of the > 1450 globally threatened bird species (Vulnerable, Endangered or Critically Endangered) are insular and are negatively affected by invasive species (BirdLife International 2017a).

Gough Island (40°03′S, 9°09′W), part of the United Kingdom Overseas Territory of St Helena, Ascension and Tristan da Cunha, is a mountainous, volcanic island in the South Atlantic Ocean with an area of approximately 65 km^2. The island is uninhabited, save for a weather station operated by South Africa, and is designated as part of a UNESCO Natural World Heritage Site, a Ramsar Wetland of International Importance and a Tristan da Cunha Nature Reserve (Ryan 2007). Gough Island is an Important Bird and Biodiversity Area and is considered one of the most important seabird colonies in the world (Swales 1965, Cuthbert *et al.* 2003, BirdLife International 2017b). Seabirds remain one of the most threatened avian groups (Croxall *et al.* 2012), vulnerable to negative impacts on land – including predation (Brooke *et al.* 2017) – and at sea (Wanless *et al.* 2009, Anderson *et al.* 2011). Gough Island hosts 22 breeding seabird species, including many that are globally threatened, and is a globally important breeding site for many species, including: Grey-backed Storm Petrel *Garrodia nereis*, White-faced Storm Petrel *Pelagodroma marina*, White-bellied Storm Petrel *Fregetta grallaria*, Broad-billed Prion *Pachyptila vittata*, Kerguelen Petrel *Aphrodroma brevirostris*, Great-winged Petrel *Pterodroma macroptera*, Soft-plumaged Petrel *Pterodroma mollis*, Grey Petrel *Procellaria cinerea*, Great Shearwater *Ardenna gravis*, Subantarctic Shearwater *Puffinus elegans*, Antarctic Tern *Sterna vittata* and Brown Skua *Catharacta antarctica* (BirdLife International 2017b). The island holds almost the entire global breeding population of Critically Endangered Tristan Albatross *Diomedea dabbenena*, Endangered Atlantic Petrel *Pterodroma incerta* (Cuthbert 2004, BirdLife International 2017b) and MacGillivray's Prion *Pachyptila macgillivrayi* (Ryan *et al.* 2014, BirdLife International 2017c), internationally important populations of two Endangered albatrosses: Sooty Albatross *Phoebetria fusca* (roughly 35% of the world population) and Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos* (20%; Cuthbert *et al.* 2003, BirdLife International 2017b), as well as two endemic land-birds, Gough Finch *Rowettia goughensis* (Ryan & Cuthbert 2008) and Gough Moorhen *Gallinula comeri* (Watkins & Furness 1986).

Many mammal species have been implicated in the majority of documented insular bird species extinctions (Atkinson & Towns 2001, Courchamp *et al.* 2003, Bellard *et al.* 2016). Rodents can have devastating effects on seabird populations (Atkinson 1985, Jones *et al.* 2008, Le Corre 2008, Phillips 2010, Cuthbert *et al.* 2013a) and can also affect entire ecosystems (Kurle *et al.* 2008, Jones *et al.* 2016). Small nocturnal, burrow-nesting species, such as petrels, and other ecologically similar taxa are among the most affected by introduced predators (Phillips 2010, Towns *et al.* 2011, Buxton *et al.* 2013). The presence of terrestrial predators can also have non-lethal effects that impact the breeding population, influencing site- (Thibault 1995), colony- (Møller 1982) and mate-fidelity (Aebischer *et al.* 1995).

Terrestrial mammals were absent from Gough Island prior to the arrival of sealers in the 19th century and the subsequent introduction of House Mice *Mus musculus* (Rowe-Rowe & Crafford 1992). It has been suggested that favourable environmental conditions, low levels of predation and an absence of mammalian competitors, along with considerable inherent adaptive plasticity, led to a gradual increase in body size across the mouse population (Cuthbert *et al.* 2016). Mice on Gough Island have an average body mass of 31 g, compared with 18–22 g elsewhere (Rowe-Rowe & Crafford 1992). This growth was facilitated by the adoption of an increasingly carnivorous diet during the winter, when many seabirds breed on the island (e.g. Tristan Albatross, Grey Petrel and Atlantic Petrel) and the mice consume a considerable amount of avian material (Jones *et al.* 2003). This predation mainly affects chicks, although eggs are also taken in small numbers (Dilley *et al.*

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2015), and is particularly severe for species that breed in winter (e.g. Tristan Albatross, Atlantic Petrel) when alternative mouse food sources, such as invertebrates, seeds and fruits, are less abundant (Davies *et al.* 2015, Dilley *et al.* 2015). This has resulted in low burrow occupancy (Cuthbert *et al.* 2013a) and low breeding success (Wanless *et al.* 2012, Dilley *et al.* 2015) among many species, which is driving significant population declines (Wanless *et al.* 2009, Cuthbert *et al.* 2014, Davies *et al.* 2015). Consequently, Gough Island has been designated the highest priority island for the removal of introduced vertebrates among UK Overseas Territories (Dawson *et al.* 2015).

We compare the breeding success of several seabird species on Gough Island with those of conspecifics and/or ecologically analogous species (hereafter termed 'analogues') from islands free of invasive terrestrial predators. We predicted that rates of breeding success of birds on Gough would be significantly lower than those of analogues, particularly among small burrow-nesting species. We also predicted that: (i) winter-breeding species will exhibit lower breeding success than summer-breeding species because mice have fewer alternative food sources in winter (Cuthbert & Hilton 2004); and (ii) below-ground nesters will have lower breeding success than surface nesters due to their smaller body sizes (Cuthbert *et al.* 2013a).

METHODS

Focal species and analogues

Estimates of the annual numbers of breeding pairs for 10 seabird species breeding on Gough Island were taken from the literature (Cuthbert & Sommer 2004, Cuthbert *et al.* 2014, Rexer-Huber *et al.* 2014, Davies *et al.* 2015) or from the authors' unpublished data (Table 1). Six of those 10 species nest in burrows, caves or crevices below-ground: Atlantic Petrel, Grey Petrel, Soft-plumaged Petrel, Great Shearwater, Broad-billed Prion and MacGillivray's Prion. Four species nest above-ground: Atlantic Yellow-nosed Albatross, Tristan Albatross, Sooty Albatross and Southern Giant Petrel. Estimates of mean (± sd) breeding success were taken from the literature and the authors' unpublished data (Table 2). Breeding success was defined as the proportion of nests that successfully fledged a chick; all species considered lay a single egg per breeding attempt.

Analogues were chosen based on comparisons of body size, ecology, sample size and life-history. Seven species were selected from the 23 candidate species identified: Antarctic Prion *Pachyptila desolata* for the two prion species, Great-winged Petrel *Pterodroma macroptera* for Atlantic Petrel, White-chinned Petrel *Procellaria aequinoctialis* for Grey Petrel, Sooty Shearwater *Ardenna grisea* for Great Shearwater, Light-mantled Albatross *Phoebetria palpebrata* for Sooty Albatross, Buller's Albatross *Thalassarche bulleri* for Atlantic Yellow-nosed Albatross, and Wandering Albatross *Diomedea exulans* for Tristan Albatross (Table 2). All analogue breeding estimates were derived from studies conducted on islands that were free of terrestrial predators (herein 'predator-free'), except for Great-winged Petrels on Marion Island, data for which were collected immediately following the eradication of feral cats when no chicks were lost to House Mice, the only remaining introduced predator (Cooper & Fourie 1991). For the two prion species we selected the Antarctic Prion because although van Rensburg and Bester (1988) reported breeding success estimates for Salvin's Prions *Pachyptila salvini* on Marion Island within predator-free enclosures, these data were collected during a single year, compared with 3 years for Antarctic Prions (Liddle 1994), which allowed the incorporation of temporal variability of breeding success in the analogue species.

Data analysis

For each species, annual rates of breeding success and associated standard distributions (sd) were used to generate a bootstrapped normal distribution (n = 1000) from which maximum and minimum breeding success estimates were extracted. Normal distributions were generated using a modified version of the core R function, *rnorm*, which required three parameters: n (sample size), $\bar{x}$ (sample mean) and s (sample standard deviation). However, maximum chick survival estimates derived from a normal distribution based on standard deviations greatly exceeded the number of breeding pairs in all instances, a problem as all the studied species lay only one egg per breeding attempt. Rather than truncate data on an *ad hoc* basis, normal distributions were generated based on standard errors; the generated distributions described the uncertainty around the mean measurement rather than the distribution of breeding

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Table 1. Reproductive success (i.e. the number of surviving chicks) of 10 seabird species on Gough Island based on observed, species-specific breeding success and that of analogue species from islands free of introduced predators (see Table 2).

Species	Population size (breeding pairs per year)	Number of surviving chicks (± 95% CI)		
		Gough Island	Analogues from islands free of introduced predators	Difference
Tristan Albatross	2000[1]	550 (400–700)	1250 (1500–1400)	700 (650–750)
Southern Giant Petrel	250[2]	150 (110–190)	180 (150–200)	30 (0–50)
Sooty Albatross	3500[2]	1000 (1000–2000)	2000 (0 – 3000)	0 (0–1000)
Atlantic Yellow-nosed Albatross	5000[2]	3000 (3000–4000)	3 000 (3000–4000)	0 (0–1000)
Grey Petrel	10 000[3]	4000 (3000–5000)	5000 (2000–8000)	2000 (0–4000)
Great Shearwater	1 000 000[4]	490 000 (345 000–650 000)	610 000 (245 000–980 000)	120 000 (0–337 000)
Atlantic Petrel	900 000[5]	270 000 (14 000–504 000)	540 000 (348 000–763 000)	270 000 (243 000–301 000)
Soft-plumaged Petrel	400 000[4]	136 000 (0–258 000)	240 000 (137 000–326 000)	104 000 (61 000–152 000)
Broad-billed Prion	875 000[4]	26 000 (0–104 000)	656 000 (511 000–781 000)	630 000 (578 000–674 000)
MacGillivray's Prion	875 000[4]	44 000 (0–192 000)	656 000 (556 000–774 000)	612 000 (584 000–645 000)
Total (to nearest 1000)	4 070 750	974 700 (366 510–1 719 890)	2 714 000 (1 803 000–3 641 000)	1 739 000 (1 467 000–2 116 000)

Species are listed in order of adult body mass. Estimates were rounded to the nearest thousand breeding pairs, except for Tristan Albatross and Southern Giant Petrel, which were rounded to the nearest 50 breeding pairs. Confidence intervals (CI) for differences between Gough species and analogues were derived from the differences between breeding success estimates, except for total difference, which was summed across all species. Upper and lower CI thresholds were defined *a priori* based on the requirement that maximum chick survival did not exceed the number of breeding pairs and that minimum chick survival was ≥ 0. [1]Davies *et al.* (2015). [2]Cuthbert *et al.* (2014). [3]Ryan (2007). [4]Cuthbert (2004). [5]Rexer-Huber *et al.* (2014).

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Table 2. Reproductive success estimates (chicks fledged per pair; RS ± standard deviation (sd)) and adult body mass of 33 seabird species from predator-free islands that were considered as candidate analogue species for those present on Gough Island.

	Species	RS ± sd	*n*	Adult mass (g)[45]
Atlantic Petrel	***Pterodroma incerta***	**0.30 ± 0.18**[1,2,3,4]	**5**	**520**
Soft-plumaged Petrel	***Pterodroma mollis***	**0.34 ± 0.18**[3,5,6]	**3**	**310**
Bonin Petrel	*Pterodroma hypoleuca*	0.82 ± 0.11[7]	6	170
Chatham Petrel	*Pterodroma axillaris*	0.64 ± 0.22[8]	19	165
Gould's Petrel	*Pterodroma leucoptera*	0.41 ± 0.15[9]	16	155
Great-winged Petrel	*Pterodroma macroptera*	0.60 ± 0.10[10]	1	530
Pycroft's Petrel	*Pterodroma pycrofti*	0.59 ± 0.05[11]	8	160
Grey Petrel	***Procellaria cinerea***	**0.36 ± 0.08**[3,12,13]	**5**	**1100**
White-chinned Petrel	*Procellaria aequinoctialis*	0.54 ± 0.10[14,15]	1	1200
Southern Giant Petrel	***Macronectes giganteus***	**0.66 ± 0.12**[6,13]	**7**	**4400**
Northern Giant Petrel	*Macronectes halli*	0.77 ± 0.15[16]	7	4300
Southern Giant Petrel	*Macronectes giganteus*	0.70 ± 0.06[8,16,17]	7	4400
Great Shearwater	***Ardenna gravis***	**0.49 ± 0.11**[3,5,6]	**6**	**850**
Hutton's Shearwater	*Puffinus huttoni*	0.46 ± 0.13[18]	9	360
Little Shearwater	*Puffinus assimilis*	0.30 ± 0.01[19]	1	225
Macronesian Shearwater	*Puffinus baroli*	0.68 ± 0.08[20]	4	–
Manx Shearwater	*Puffinus puffinus*	0.61 ± 0.16[21,22]	26	455
Short-tailed Shearwater	*Ardenna tenuirostris*	0.82 ± 0.05[23]	6	560
Sooty Shearwater	*Ardenna grisea*	0.61 ± 0.26[24,25]	33	790
Wedge-tailed Shearwater	*Ardenna pacificus*	0.47 ± 0.31[26,27]	11	390
Broad-billed Prion	***Pachyptila vittata***	**0.03 ± 0.05**[3,5]	**3**	**200**
Macgillivray's Prion	***Pachyptila macgillivrayi***	**0.05 ± 0.09**[3,13]	**3**	**190**[†]
Antarctic Prion	*Pachyptila desolata*	0.76 ± 0.07[28]	3	150
Salvin's Prion	*Pachyptila salvini*	0.66 ± 0.09[29]	2	200
Slender-billed Prion	*Pachyptila belcheri*	0.57 ± 0.19[30,31,32]	17	145
Atlantic Yellow-nosed Albatross	***Thalassarche chlororhynchos***	**0.63 ± 0.12**[2,6,33]	**32**	**2200**
Black-browed Albatross	*Thalassarche melanophris*	0.34 ± 0.18[34,35]	19	3600
Buller's Albatross	*Thalassarche bulleri*	0.69 ± 0.16[36,37]	9	2800
Grey-headed Albatross	*Thalassarche chrysostoma*	0.39 ± 0.16[38]	17	3500
Sooty Albatross	***Phoebetria fusca***	**0.42 ± 0.07**[2,6,13]	**9**	**2500**
Light-mantled Sooty Albatross	*Phoebetria palpebrata*	0.47 ± 0.07[39]	1	3150
Tristan Albatross	***Diomedea dabbenena***	**0.28 ± 0.09**[2,13,40,41,42]	**13**	**7000**
Wandering Albatross	*Diomedea exulans*	0.63 ± 0.05[43,44]	10	8200

Gough Island species are given in bold; selected analogues are underlined. It was not possible to derive sd for several analogue species, and thus sd for Great-winged Petrel and White-chinned Petrel were calculated as a mean across all analogue species sd values, and Light-mantled Albatross were assigned the same sd value as Gough Island Sooty Albatross. *n* = number of breeding success estimates. [1]Cuthbert (2004). [2]Cuthbert and Hilton (2004). [3]Dilley *et al.* (2015). [4]Wanless *et al.* (2012). [5]Cuthbert *et al.* (2013a,b, 2014). [6]Cuthbert *et al.* (2014). [7]Seto and Conant (1996)*. [8]Gummer *et al.* (2015). [9]Department of Environment and Conservation (NSW) (2006)**. [10]Cooper and Fourie (1991)***. [11]Pierce (2002). [12]Cuthbert *et al.* (2013a,b, 2014). [13]RSPB unpublished. [14]Hall (1987). [15]Berrow *et al.* (2000). [16]Hunter (1984). [17]Quintana *et al.* (2006). [18]Cuthbert and Davis (2002). [19]Booth *et al.* (2000). [20]Fagundes *et al.* (2016). [21]Brooke (1978). [22]Thompson and Furness (1991). [23]Einoder *et al.* (2013). [24]Newman *et al.* (2009). [25]Geary *et al.* (2014). [26]Floyd and Swanson (1983). [27]Hill *et al.* (1996). [28]Liddle (1994). [29]van Rensburg and Bester (1988)****. [30]Quillfeldt *et al.* (2003). [31]Quillfeldt *et al.* (2007). [32]Nevoux and Barbraud (2006). [33]Cuthbert *et al.* (2003). [34]Kirkwood and Mitchell (1992)‡. [35]Croxall *et al.* (1988)‡. [36]Sagar *et al.* (2002). [37]Sagar and Warham (1998). [38]Prince *et al.* (1994). [39]Thomas *et al.* (1983). [40]Davies *et al.* (2015). [41]Wanless et al. (2007). [42]Wanless *et al.* (2009). [43]Weimerskirch and Jouventin (1987). [44]Croxall *et al.* (1990). [45]Dunning (2008). [†]Ryan (unpubl data). *Rodent control. **Predator control & habitat management. ***Post-cat eradication. Chick mortality = 0. ****Predator-free enclosures. [‡]RS = chicks raised to 5 weeks of age.

success rates for each species. Furthermore, *rnorm* was modified to constrain upper and lower breeding success estimates to 0 and 1, respectively, thus limiting inflation beyond biologically realistic boundaries. Derived population estimates were rounded to the nearest 1000 breeding pairs, except for Tristan Albatross and Southern Giant Petrel (nearest 50) and their analogues (Table 1). Breeding success rates (i.e. mean, maximum, minimum) were used to calculate the number of surviving chicks for each Gough – analogue species pair and the differences between the two.

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Table 3. Generalized linear mixed model (GLMM) results for variables affecting the breeding success of 10 seabird species on Gough Island.

Model	AIC	ΔAIC	Variable	β (± se)
RS ~ *n* + *w* + (*y*) + (*s*)	**64.25**	0.00	*n*	−4.91 ± 1.7**
			w	−3.74 ± 2.0
RS ~ *s* + *n* + *w* + (*y*) + (*s*)	65.98	1.73	*s*	0.10 ± 0.2
			n	−5.11 ± 1.7**
			w	−4.60 ± 2.7
RS ~ *n* + *b* + *w* + (*y*) + (*s*)	66.22	1.96	*n*	−4.73 ± 1.9*
			b	−0.17 ± 0.9
			w	−3.44 ± 2.5
RS ~ *n* + (*y*) + (*s*)	66.22	1.96	*n*	−2.72 ± 0.7***
RS ~ *n* + *b* + (*y*) + (*s*)	66.32	2.07	*n*	−2.61 ± 0.7***
			b	−0.96 ± 0.7
RS ~ *s* + *n* + (*y*) + (*s*)	67.41	3.16	*s*	−0.12 ± 0.1
			n	−2.95 ± 0.8***
RS ~ *s* + *n* + *b* + (*y*) + (*s*)	67.66	3.41	*s*	−0.11 ± 0.1
			n	−2.93 ± 0.9***
			b	−0.91 ± 0.7
RS ~ *s* + *n* + *b* + *w* + (*y*) + (*s*)	67.97	3.71	*s*	0.11 ± 0.2
			n	−5.25 ± 2.2*
			b	−0.06 ± 0.1
			w	−4.20 ± 3.7
RS ~ *s* + *b* + *w* + (*y*) + (*s*)	74.12	9.91	*s*	−0.21 ± 0.1
			b	−2.05 ± 0.7**
			w	4.28 ± 1.5**
RS ~ *b* + *w* + (*y*) + (*s*)	74.35	10.09	*b*	−1.95 ± 0.7**
			w	2.85 ± 1.1*
RS ~ *b* + (*y*) + (*s*)	80.22	15.96	*b*	−1.25 ± 0.6*
RS ~ *w* + (*y*) + (*s*)	80.55	16.30	*w*	2.33 ± 1.4
RS ~ *s* + *w* + (*y*) + (*s*)	80.84	16.58	*s*	−0.16 ± 0.1
			w	3.26 ± 1.5*
RS ~ *s* + *b* + (*y*) + (*s*)	81.19	16.94	*s*	0.10 ± 0.1
			b	−1.51 ± 0.7*
RS ~ (*y*) + (*s*)	82.41	18.16		
RS ~ *s* + (*y*) + (*s*)	84.38	20.11	*s*	0.02 ± 0.1

RS = reproductive success (square root-transformed); *s* = species; *n* = nesting location (above or below ground); *b* = breeding season (summer or winter); *w* = adult body mass (g); *y* = year. Variables in parentheses were fitted as random factors. Models are ranked according to their Akaike's information criterion (AIC) value; the top-ranked model is given in bold. Models within the top subset (ΔAIC < 2) were included in the average model (Table 4). Regression coefficients (β ± se) and significance of contributory variables are given, where *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

Factors affecting the breeding success of Gough Island species – including differences between summer- and winter-breeding species and between above- and below-ground nesting species – were investigated using general linear mixed models (GLMMs) where breeding success was fitted as the response variable, nesting location (above/below ground), breeding season (summer/winter) and adult body mass (standardized to zero mean and unit variance to facilitate model convergence) were fitted as explanatory variables, and species and the year of data collection were fitted as random factors. Variance inflation factors (VIFs) for explanatory variables were < 3 (Zuur *et al.* 2010), supporting their inclusion. It was necessary to apply a square root transformation to the response variable to satisfy GLMM assumptions. Models were assessed using Akaike's information criterion (AIC; Akaike 1973, 1974, Burnham & Anderson 2002). Model averaging was used to derive the best approximating unconditional model incorporating all variables from the top subset of all models (ΔAIC < 2; Table 3). Differences between Gough – analogue pairs were investigated using an individual GLMM where breeding success was fitted as the response variable, location (i.e. Gough Island or non-Gough islands) was fitted as an explanatory variable, and species and year of data

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collection were fitted as random factors. As with Gough-only models, the response variable was square root-transformed to meet model assumptions.

To calculate the difference in the number of chicks raised to fledging between Gough – analogue pairs, the estimated population size of a single focal species on Gough Island was multiplied by the difference between its breeding success and that of its predator-free analogue. The total putative impact of House Mice was then calculated as the sum of differences in the number of chicks raised to fledging across all Gough Island species relative to analogues:

$$\Sigma n_i = \left(\mathrm{RS}_{\mathrm{if}} - \mathrm{RS}_{\mathrm{ig}}\right) \times D_{\mathrm{ig}}$$

where n = total number of chicks per species, RS = reproductive success rates, D = estimated population size on Gough Island, f = predator-free islands, g = Gough Island, for a given Gough – analogue pair (i). Owing to the significant predation on Gough, and declining populations, we did not consider density-dependent effects on breeding success. A chi-square goodness-of-fit test was used to investigate differences between Gough – analogue pairs. All data analyses were conducted in R version 3.4.3 (R Core Team 2017, see Caravaggi *et al.* 2018 for data and code).

RESULTS

Most seabirds on Gough Island had lower breeding success compared with analogues from predator-free islands. Broad-billed Prions had the lowest breeding success on Gough, only 3% that of the analogue species. Conversely, estimates of breeding success were similar for three summer-breeding, surface-nesting Gough – analogue pairs: Southern Giant Petrel, Atlantic Yellow-nosed Albatross and Sooty Albatross and their analogues (Table 2).

The top-ranked model comparing breeding success among species nesting on Gough Island consisted of nesting location (AIC = 64.26), where below-ground nesters had lower breeding success than above-ground nesters, and adult body mass, where lighter species had greater losses. Five models were identified as occurring within the top subset (ΔAIC < 2; Table 3) and, hence, were used in generating model-averaged parameter estimates. Nesting location exerted the strongest influence on the best approximating average model (importance = 1), followed by adult body mass (0.64). Breeding season and species were less important within the average model (0.35 and 0.32, respectively; Table 4).

There was a difference between Gough – analogue pairs with analogue species having higher breeding success than those on Gough Island ($\beta = 2.44 \pm 0.62$, $P < 0.0001$). Population estimates based on bootstrapped normal distributions, derived from mean breeding success and associated confidence intervals, revealed significantly fewer chicks raised to fledging in seven of the 10 Gough Island species analysed compared with analogues ($\chi^2 = 552.780$, df = 9, $P < 0.0001$). Of the more than 4 million breeding pairs of the species included in our dataset, fewer than 1 million (best estimate 974 700; 366 510–1 719 890) successfully raised chicks to fledging on Gough, whereas using breeding success estimates for analogues from predator-free islands suggests that the subset of seabirds from Gough Island used in this analysis should have had an annual production of almost 3 million chicks (2 714 000; 1 803 000–3 641 000), a difference of close to 2 million chicks per year (1 739 000; 1 467 000–2 116 000; Table 1). After omitting the three species for which there is little evidence of mouse predation (Atlantic Yellow-nosed Albatross, Sooty Albatross and Southern Giant Petrel), we found that an average of 25% of breeding pairs successfully raised chicks to fledging, 60% fewer than would be expected (Table 1).

Of the three species entirely, or almost entirely, restricted to Gough Island, MacGillivray's Prions had a breeding success of 0.05 ± 0.09 (Fig. 1), raising more than half a million (584 000–645 000) fewer chicks to fledging than might be

Table 4. Model averaging results (unconditional, full-model) for variables affecting the breeding success of 10 seabird species on Gough Island.

Variable	Importance	β (± se)
Nesting location (below-ground)	1.00	−4.54 ± 1.82*
Adult body mass (g)	0.64	−3.88 ± 2.35
Breeding season (winter)	0.35	−0.17 ± 0.87
Species	0.32	0.10 ± 0.19

Constituent models were selected based on their occurrence within the top subset of all models (ΔAIC < 2; Table 3). Species and the year in which data were collected were fitted as random factors. Regression coefficients (β ± se) and significance of contributory variables are given, where *P < 0.05.

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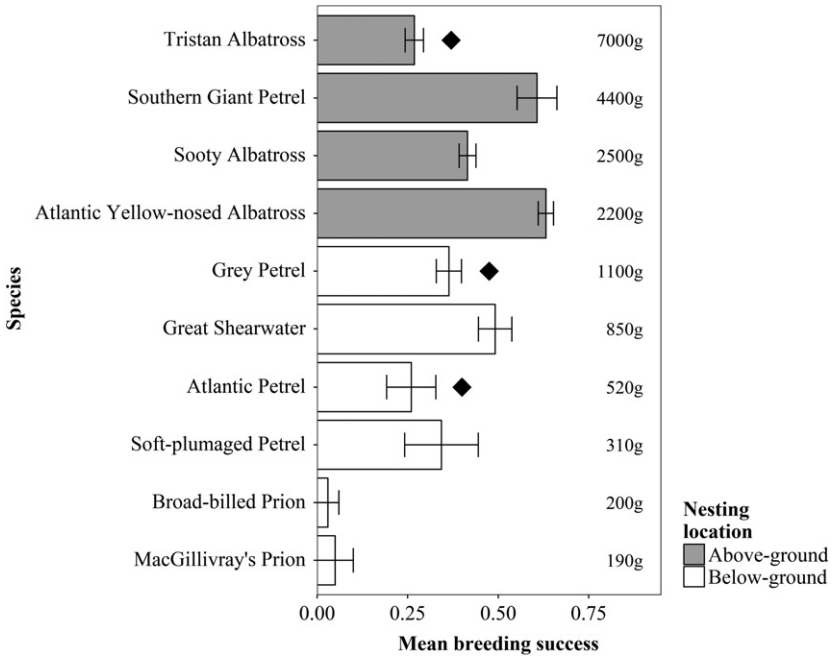


Figure 1. Mean breeding success (± se) of above-ground and below-ground breeding seabirds on Gough Island. Species are listed in order of adult body mass (given, right). ♦ Winter-breeding species (all others breed in the summer).

possible in a predator-free environment (Table 1). The breeding success of Atlantic Petrels was 0.30 ± 0.18 (Fig. 1), resulting in over 300 000 fewer chicks (243 000–301 000; Table 1) and Tristan Albatross breeding success was 0.28 ± 0.09 (Fig. 1), with 700 (650–750; Table 1) fewer chicks being raised each year, a comparative reduction of 35 ± 2.5%.

DISCUSSION

The breeding success of many breeding seabird species on Gough Island, in particular burrowing (i.e. below-ground nesting) petrels, was extremely poor when compared with analogue species from islands without introduced mammalian predators, and approximately 2 million fewer chicks were raised among all studied species annually than would be expected in an introduced predator-free environment. If predation rates have remained constant over the last few decades, this number would have been even greater in previous years when seabird populations on the island were larger (e.g. Cuthbert *et al.* 2013a,b, 2014). Previous studies have suggested that depredation of certain individual species by mice results in the death of nearly 60% of all chicks annually on Gough (Wanless *et al.* 2012, Cuthbert *et al.* 2013a, Davies *et al.* 2015, Dilley *et al.* 2015). However, the impacts we estimated are more severe, with only 33% of pairs raising chicks to fledging, across 10 studied species. Winter-breeding burrowing petrels were the most affected, particularly the smaller species and those with chicks that hatched in late winter, such as the Atlantic Petrel. It is highly likely that other winter burrow-nesting species such as the Great-winged Petrel are or have been similarly impacted on the island, particularly given the historical abundance of a number of species that are now locally scarce (Swales 1965, Dilley *et al.* 2015). Given that there are no data on breeding success for nearly half of the 23 species breeding on Gough, many of which are small, increasingly scarce burrow-nesting species (e.g. storm petrels) that are likely to be severely affected by mice (Cuthbert *et al.* 2013a, Newton *et al.* 2016), our estimate of predation is an underestimate, and the number of chicks and eggs putatively depredated by mice is likely to exceed 3 million annually.

Our main purpose was to estimate the putative impacts of mice on the breeding success of Gough Island seabird populations and it is impossible to derive such data without comparators. As there

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are no data available relating to the breeding success of seabirds on Gough Island before the introduction of House Mice in the 19th century, we used taxonomically related and ecologically and morphologically similar species for comparisons. There are few data available on the breeding success of such species on islands that are free of invasive predators, so our pool of potential analogues was limited. Moreover, many of the focal species from Gough Island are endemic or near-endemic, necessitating our use of congeneric analogues. By incorporating the random variance from predator-free sites through bootstrapping, and modelling study year as a random factor in our models, we incorporated estimates of uncertainty throughout our analyses. Until breeding success can be measured on a mouse-free Gough Island, we believe this is the most defensible, robust approach to the question of how many chicks are depredated by mice on Gough Island annually. Given the population declines observed in many species (Cuthbert *et al.* 2014, Rexer-Huber *et al.* 2014, Davies *et al.* 2015), we do not believe nesting habitat is limiting, and consequently density-dependent effects on breeding success are unlikely to be responsible for the differences we observed. Other potential factors include outbreaks of disease (e.g. Weimerskirch 2004), variations in prey availability (Becker *et al.* 2007), extreme weather events (Frederiksen *et al.* 2008) and industrial fishing activity (Genovart *et al.* 2017). The subterranean burrows in which many species breed provide a relatively stable microclimate, buffering extreme weather events, and therefore the differences in breeding success are unlikely to be attributable to weather. Similarly, there has been no evidence of disease outbreaks in any species studied on Gough Island. In contrast, industrial longline fisheries may be responsible for an annual decline of up to 2.5% in the Tristan Albatross population (Wanless *et al.* 2009). Prey availability is unlikely to be a significant factor given the large range over which species forage, and the degree of marine protection in the Tristan da Cunha Exclusive Fisheries Zone (Caselle *et al.* 2018).

The chicks of winter-breeding species are generally considered to be more susceptible to predation by mice because there are fewer alternative food sources available to mice during winter (Cuthbert & Hilton 2004) when mice are food-limited (Cuthbert *et al.* 2016). Great Shearwater, a summer-breeding surface-nesting species, also had reduced breeding success relative to the analogue species. Although Great Shearwater chicks weigh up to 1000 g, they are considerably smaller at fledging than those of surface-nesting albatrosses and Southern Giant Petrels and may be therefore more vulnerable to mouse predation. This hypothesis is potentially confounded by the fact that Tristan Albatross chicks (~ 10 000 g) are subject to extremely high predation rates. However, Tristan Albatross breed during winter, and their chicks are mainly attacked by mice when *per capita* food availability for mice is depressed (e.g. Cuthbert *et al.* 2016, Parkes 2016). Therefore, mice may be driven to exploit all potential resources during winter, including chicks of larger species such as Tristan Albatross. Furthermore, while population-level impacts on Atlantic Yellow-nosed Albatross are low, local impacts can be considerable (Cuthbert *et al.* 2013b).

Smaller summer-breeding species, such as MacGillivray's Prion, are also affected significantly. The extent of the impacts on MacGillivray's Prion gives considerable cause for concern and is probably typical of impacts on other small burrow-nesting species such as Subantarctic Shearwater, Common Diving Petrel *Pelecanoides urinatrix* and the three species of storm petrels for which there are no breeding success data, in large part because they have become so rare on the island over the last few decades (Ryan 2010). Breeding success of Atlantic Yellow-nosed Albatross, Sooty Albatross and Southern Giant Petrel, which breed in the spring and summer, was similar to those of analogues. Although mice prey on chicks of these species, this is relatively uncommon (Cuthbert *et al.* 2013b). However, mice can alter their predation tactics rapidly, impacting previously unaffected species (Dilley *et al.* 2016). Wanless *et al.* (2009) suggested that predation by mice played a significant role in the 50% decrease in breeding Tristan Albatrosses over the preceding 50 years but impacts previously went unnoticed or were misattributed. There may be a similar scenario unfolding among summer-breeding species on Gough, raising the possibility that many more species are threatened by mouse predation, particularly the small burrowing petrels.

The focal suite of species includes three that are *de facto* endemics, as more than 99% of their breeding populations are restricted to Gough Island: MacGillivray's Prion, Atlantic Petrel and Tristan Albatross. MacGillivray's Prion had the

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lowest breeding success of any species (5%) with the exception of the Broad-billed Prion (3%), and has experienced high rates of chick mortality in recent years due to predation by mice, including complete breeding failure at one study site in 2014–2015 (cave site; Dilley *et al.* 2015) and 2015–2016 (present authors' unpubl. data). This is in stark contrast to the mean chick survival rate (0.75 ± 0.08) of the analogue species on predator-free Bird Island, South Georgia (Liddle 1994). Similarly, Atlantic Petrel and Tristan Albatross had very low productivity, with breeding success considerably lower than that of analogues. Previous studies have suggested that mice are driving population declines in both species (Cuthbert 2004, Wanless *et al.* 2009) and that the degree of predation is unsustainable (Cuthbert *et al.* 2013b). The Tristan Albatross is particularly imperilled as its population is declining by 3% per year (Cuthbert *et al.* 2014). Annual recruitment of 162 individuals per year, or 30% of fledged chicks (e.g. Croxall *et al.* 1990), not accounting for post-fledging mortality, is insufficient to allow for effective population recovery in the long-term if such high levels of predation continue. Our findings have serious implications for the long-term future of these near-endemic species on Gough Island, which, without the eradication of mice, will probably become extinct.

The impacts of mice on the avifauna of Gough Island, including the Critically Endangered, endemic Gough Finch (Ryan & Cuthbert 2008) are increasingly well documented (Cuthbert & Hilton 2004, Wanless *et al.* 2012, Cuthbert *et al.* 2013a, Davies *et al.* 2015, Dilley *et al.* 2015) and there have been many calls for mouse eradication from the island. The eradication is technically feasible, and planning is underway (Parkes 2008, Cuthbert *et al.* 2011a,b, Royal Society for the Protection of Birds (RSPB) 2017). Rodents have been successfully removed from many islands worldwide, frequently resulting in the recovery of native avifauna, including increased breeding success, recruitment and population growth (Lavers *et al.* 2010, Jones *et al.* 2016, Brooke *et al.* 2017). Immigration is a significant predictor of population growth following invasive predator removal (Buxton *et al.* 2014, Brooke *et al.* 2017), potentially limiting the recovery of endemic species, particularly those with small populations, such as Tristan Albatross, although there are some exceptions (e.g. Ryan *et al.* 2006). Post-eradication monitoring is therefore critical in evaluating not only the success of eradication efforts but also the demographic responses of affected seabirds. Moreover, more than one conservation strategy may be required to effectively conserve particularly imperilled species (e.g. Lavers *et al.* 2010). The recovery of Tristan Albatrosses, for example, requires a reduction in bycatch at sea, as well as the eradication of mice (Wanless *et al.* 2009).

Albatrosses and many burrowing petrels have long lifespans, low fecundity and do not reach sexual maturity until they are several years old (Brooke 2004). These traits confer limited resilience to decreases in adult survival (e.g. via accidental bycatch in fisheries; Nel *et al.* 2002, Barbraud *et al.* 2009) but they also facilitate the persistence of a population in the face of high predation pressure on early life-history stages, even with significantly reduced recruitment. However, mice impact seabirds on Gough by killing chicks in large numbers. The magnitude of annual losses sustained by seven of the focal species analysed in this study is of considerable concern. Many may be reduced to relict populations, if not extirpated from the island entirely, should such high-intensity predation continue or increase. Therefore, the long-term futures of several species on Gough Island are dependent, at least in part, on the eradication of mice such that recruitment and replacement of ageing birds in breeding populations can occur in the short- to medium-term.

Mice are the most important factor in avian population declines on Gough Island. Small burrowing petrels such as Endangered Atlantic Petrel and Endangered MacGillivray's Prion, along with Critically Endangered Tristan Albatross, are likely to be driven to extinction on Gough if mice are not eradicated. Fortunately, examples from invasive predator eradication programmes elsewhere suggest that recovery is possible post-eradication (Jones 2010, Brooke *et al.* 2017). Monitoring future trends in breeding parameters is crucial in establishing the recovery potential of the Gough Island seabird populations and facilitating the development of conservation measures aimed at preserving its endemic species.

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