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Short communication

The depth of Sooty Shearwater *Ardenna grisea* burrows varies with habitat and increases with competition for space

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The Sooty Shearwater *Ardenna grisea*, an abundant but declining petrel, is one of many seabird species that construct breeding burrows, presumably because these confer protection from predators and the elements. Little is known about the causes of variation in Sooty Shearwater burrow architecture, which can differ markedly both within and between breeding sites. We hypothesize that burrow architecture varies in response to habitat type and competition for space. To address these hypotheses, we recorded Sooty Shearwater burrow dimensions on Kidney Island, the largest Sooty Shearwater colony in the Falkland Islands, South Atlantic, and modelled these as functions of burrow density (a proxy for competition) and habitat indices. Our models suggest that Sooty Shearwaters burrow further underground in response to competition for breeding space, and that soil underlying dense tussac grass *Poa flabellata* is more easily excavated than other substrates, indicating how vegetation restoration could aid the conservation of this species.

Keywords: burrow dimensions, burrowing petrels, Falkland Islands, nest architecture, *Puffinus griseus*.

Many seabirds, including most small-medium Procellariiformes (hereafter 'petrels'), as well as many alcids and some penguins, breed in burrows. Yet, burrows are energetically costly to build and can be subject to flooding, collapse and other disadvantages (Warham 1996). Therefore, the advantages of protection from predators and climatic extremes must outweigh the costs of burrow nesting. Burrow nesting by seabirds can have wider effects, such as modifying the structure and nutrient content of island soils, which can then cascade to other trophic levels (Bancroft *et al.* 2005). In other fossorial animals, the impact of these processes depends in part on the structure of the burrow systems (Laundré & Reynolds 1993). Some petrels, such as the White-chinned Petrel *Procellaria aequinoctialis* or the Flesh-footed Shearwater *Ardenna carneipes* construct relatively simple and straight burrows (Parker & Rexer-Huber 2015). Conversely, the burrows of others, such as the Sooty Shearwater *Ardenna grisea*, are longer and complex, sometimes with multiple entrances and bifurcations (Warham 1996, Hamilton 2000). However, little is known about the drivers of variation in seabird burrow architecture.

One potential driver is competition for space; that is, to obtain a breeding territory in a crowded area, birds may dig further underground (Warham 1996, Ramos *et al.* 1997). In addition, it is likely that burrow characteristics vary with habitat, such as vegetation, slope, soil structure or type, as these will affect both the energetic cost of excavation and the structural and hydrological properties of the burrow (Ramos *et al.* 1997, Powell *et al.* 2007). Neither of these hypotheses has been tested.

The Sooty Shearwater is an abundant but declining burrowing petrel. It is currently listed as Near-threatened, in part due to loss of breeding habitat (Scott *et al.* 2008). Sooty Shearwaters prefer to breed under dense vegetation, including tussac grasses *Poa* spp., and small trees, e.g. tree daisies *Olearia* spp. (Scott *et al.* 2009, Geary *et al.* 2014, T.J. Clark *et al.* unpubl. data). It has been suggested that the loss of the tussac grass *Poa flabellata* caused a reduction in Sooty Shearwater breeding populations in the Falkland Islands (T.J. Clark *et al.* unpubl. data). Sooty Shearwater burrows may extend to 3 m in length, sometimes comprising labyrinthine systems (Hamilton 2000). Burrow architecture can vary considerably between and within colonies. For example, burrows at Putauhinu Island, New Zealand, are on

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average 0.5 m longer (McKechnie *et al.* 2007) than those at Tītī Island, New Zealand (Geary *et al.* 2014). It is not known whether this is due to differences in habitat or competition.

Here, we test whether the architecture (i.e. burrow entrance width, height and burrow length) of Sooty Shearwater burrows on Kidney Island, Falklands Islands, varies with competition and habitat. Understanding the drivers of variation in burrow architecture could inform habitat restoration projects as well as studies on competition and nutrient cycling by seabirds.

METHODS

We carried out fieldwork from 7 to 21 January 2017 on Kidney Island (51.6238°S, 57.7520°W), which is approximately 0.32 km^2 in area and is largely covered in dense tussac grass. Kidney Island has been designated as an Important Bird Area and National Nature Reserve by the Falkland Islands Government (Kidney Island Group 2006), principally because it is the main breeding site for Sooty Shearwaters in the South Atlantic, with a population size of approximately 140 000 breeding pairs (T.J. Clark *et al.* unpubl. data).

We established 66 study plots by projecting a regular 50 × 75 m grid over a polygon delimitating the vegetated area of Kidney Island. At each grid node, we set out a circular plot of 2.5 m radius (i.e. *c.* 20 m^2). We estimated burrow density, which we assume to be a proxy for competition for space, by counting the number of burrows in each plot, ignoring those < 40 cm long, which Scott *et al.* (2008) suggested would not be viable. Initial observations showed that burrows generally tapered in the first few centimetres from the entrance, before becoming more constant. In the interests of repeatability, we defined the minimum entrance width and height as the minimum dimensions within the first 5 cm of each burrow. Within each plot, we randomly measured to the nearest centimetre the minimum entrance width and height of up to five burrow entrances (some plots contained fewer than five burrows) using measuring tape. We then recorded the following habitat variables: soil moisture, mean tussac height, percentage tussac cover and presence of protruding rock substrate. We classified soil moisture on a four-point scale: 1 (dry, well-drained), 2 (intermediate), 3 (saturated, moisture comes to the surface when pressed by hand) and 4 (standing water within the plot) (Lawton *et al.* 2006). We measured average tussac height to the nearest 0.25 m from the ground to the top of the grass, using a graduated pole. We estimated approximate per cent tussac cover by eye. We also measured the lateral length of burrows in a subsample of 18 plots, aligned along two perpendicular transects spanning the full range of breeding habitats on the island. Burrow length was measured to the nearest 10 cm using divisions marked on the flexible probe of a burrowscope (Ridgid micro CA-300 Hand-held Inspection Camera, Elyria, OH, USA). Due to the constraints of another study carried out at the same time, we only monitored single-entrance burrows, which were determined by hand. In addition, we calculated slope in QGIS 2.8.3 (QGIS Development Team 2016) using a digital elevation model (10 m resolution) retrieved from the Earthdata search portal, courtesy of NASA Land Processes Distributed Active Archive Center (NASA JPL 2013) and provided by the South Atlantic Environmental Research Institute data centre.

Tussac grass was harvested periodically on Kidney Island until the 1950s and was also damaged by a fire in the 1940s (Kidney Island Group 2006). Subsequently, it has re-grown. We estimated the change in tussac cover over time by comparing a satellite image of Kidney Island from 2017 (Google Earth Pro 2017) with an aerial image taken by the British Geological Survey in 1956, provided by the Falkland Islands Department of Mineral Resources. We estimated tussac grass coverage for each photo by extracting the grey raster band values for each sample plot in QGIS, with darker values corresponding to higher cover and lower values to lower cover. We defined the relative change in cover as the difference between the grey raster band values for the 1956 and 2017 images, with smaller absolute values indicating similar cover between the years in the images and larger absolute values indicating different cover.

White-chinned Petrels and Magellanic Penguins *Spheniscus magellanicus* breed at low densities in burrows on Kidney Island and therefore potentially compete with Sooty Shearwaters for space. We recorded the presence of these species in study plots, but found no White-chinned Petrels and only four Magellanic Penguin burrows, so we did not consider their influence further.

We modelled variation in burrow entrance width and height, and burrow length using generalized linear models (GLMs) fitted in R (R Core Team 2013), assuming Gaussian errors and an identify link function. We confirmed model assumptions of normality and homoscedasticity of residuals by examining normal quantile–quantile plots and residuals vs. fitted values, respectively. We simplified models by backwards selection using a stepwise procedure based on Akaike's information criterion (AIC; Burnham & Anderson 2003), implemented using the 'step' function in R. Beginning with the full model for each response (entrance width, entrance height or burrow length), this function determines which model term's removal would result in the greatest reduction in AIC. In the next step, this term is removed and the procedure is repeated until no reduction in AIC is possible. The 'best' model is that with the lowest AIC. For each response, the full model contained the following explanatory terms, included on the basis of biological plausibility: slope; soil moisture; tussac cover and height;

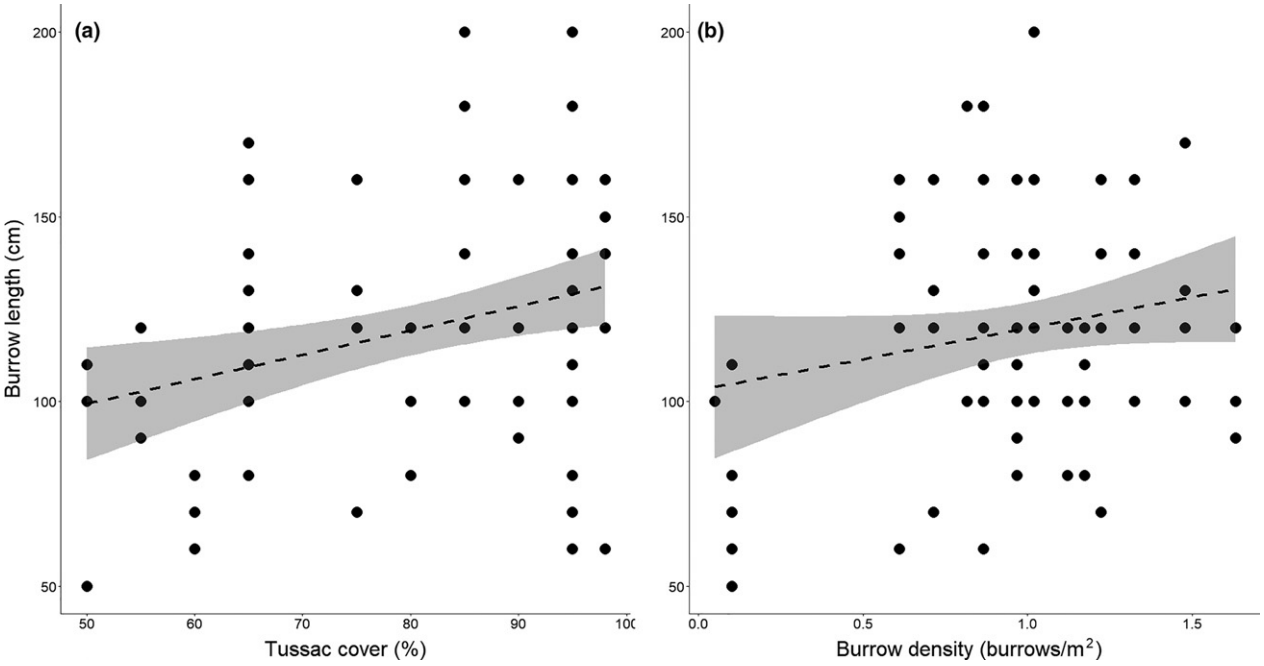

Figure 1. Relationships between observed Sooty Shearwater burrow length (cm) and (a) tussac cover (%) or (b) burrow density (burrows/m^2). The dashed line represents best model predictions and grey shading represents 95% confidence intervals.

relative change in tussac cover; presence of rock substrate; burrow density; and an interaction between tussac cover and height. To illustrate how the best models compare with their nearest competing models, we present ΔAIC for all candidate models. During exploratory analysis we considered specifying plot as a random effect, but this did not improve model performance. We therefore assume that burrows within plots are independent. In addition, we checked for residual spatial autocorrelation by calculated Moran's I for the residuals from the final models. To allow covariate effect sizes to be compared directly using parameter estimates and their associated 95% confidence intervals, we standardized covariates prior to model fitting.

RESULTS

Average burrow dimensions were: entrance width, 17.6 ± 0.3 cm (range 6–35 cm, n = 269); entrance height, 11.6 ± 0.2 cm (range 5–34 cm, n = 269); and length, 119.5 ± 3.6 cm (range 50–200 cm, n = 81). The mean burrow density was 0.60 ± 0.06 burrows/m^2 (range 0–1.73 burrows/m^2, n = 66).

The best models of both burrow entrance width (pseudo R^2 = 0.010) and entrance height (pseudo R^2 = 0.033) contained only the intercept term, indicating that these dimensions did not vary markedly with the habitat and competition indices considered (see Tables S1 and S2). In contrast, the best model of burrow length (pseudo R^2 = 0.148) predicted an increase in length with burrow density (mean effect size = 0.275; 95% confidence interval (CI) 0.026–0.524) and tussac cover (mean effect size = 0.344; 95% CI 0.129–0.539; Fig. 1). This model was clearly better than the next competing model (ΔAIC > 2; Table 1) and resulted in negligible residual spatial autocorrelation (Moran's I = −0.074, P = 0.28).

DISCUSSION

We found that Sooty Shearwater burrows were longer in areas with greater burrow density. This supports the hypothesis that burrowing seabirds respond to competition for space by digging further underground into substrate (Warham 1996). Published data on Sooty Shearwater burrow lengths in other regions are limited (Table 2) and we are circumspect about drawing comparisons between studies. First, different methods were used to measure burrow length; as in the present study, Geary *et al.* (2014) extended a burrowscope to the assumed end of the burrow, whereas others have excavated burrows to determine their length (Hamilton 2000, McKechnie *et al.* 2007). Secondly, the predominant vegetation type differed among sites (Table 2). It may be that birds crowd more and dig further in better excavation conditions (due to variability in vegetation or

Table 1. Summary of model selection results for all candidate and intercept-only models of estimating Sooty Shearwater *Ardenna grisea* burrow length on Kidney Island, Falkland Islands.

Model	No. of parameters	ΔAIC
TC + BD	3	0.000
TC + BD + TH	4	3.490
TC + BD + TH + TA	5	3.650
TC + BD + TH + TA + TC*TH	6	3.960
TC + BD + TH + TA + SL + TC*TH	7	4.220
TC + BD + TH + TA + SL + SM + TC*TH	8	5.610
TC + BD + TH + TA + SL + SM + RP + TC*TH	9	12.000
Intercept-only	1	8.800

'Intercept' contains no covariates. BD, burrow density; RP, presence of rock substrate; SL, slope; SM, soil moisture; TA, change in tussac cover; TC, tussac cover; TH, tussac height. *Interaction.

Table 2. Mean length of Sooty Shearwater burrows, burrow density and primary vegetation located on a sample of islands, sorted from low to high mean burrow density. Method used was either Burrowscope (B) or Excavation (E). Adapted from Geary *et al.* (2014).

Location	Method	Sample size	Mean burrow length ± se (cm)	Mean density ± se (burrows/m^2)	Primary vegetation	References
Long Island, Marlborough Sound, NZ	B	51	83.6 ± 4.3	0.138	Taupata (*Coprosma repens*)	Geary *et al.* (2014)
Titi Island, Cook Strait, NZ	B	34	80.6 ± 5	0.139	Taupata (*Coprosma repens*)	Geary *et al.* (2014)
Bench Island, Stewart Island, NZ	E	~40 (2 plots)[a]	132.31 ± 5.8	0.33 ± 0.20	Tupare (*Olearia lyallii*)	McKechnie *et al.* (2007)
Putauhinu Island, Stewart Island, NZ	E	~60 (3 plots)[a]	133.25 ± 3.47	0.86 ± 0.09	Tupare (*Olearia lyallii*)	McKechnie *et al.* (2007)
Kidney Island, Falkland Islands	B	81	119.5 ± 3.6	0.60 ± 0.47	Tussac grass (*Poa flabellata)*	This study
Northeast Island, The Snares, NZ	E	~100 (5 plots)[a]	102.0 ± 1.3	0.98 ± 0.30	Tupare (*Olearia lyallii)*	McKechnie *et al.* (2007)

[a]Data from an unknown number of nests in plots; range is 19–21 burrows per plot.

soil characteristics) instead of responding to conspecific density itself. Nonetheless, it can be seen that the shortest burrows occurred at the two colonies with the lowest nest density (Geary *et al.* 2014).

Other animals also build up or down in response to competition for space: fossorial rodents, such as pocket gophers (e.g. *Thomomys bottae*, *Geomys attwateri*), dig longer and more complex burrows to adapt to higher population densities (Cameron *et al.* 1988); many sessile invertebrates (e.g. mussels, barnacles and tunicates) form dense assemblages called hummocks, which grow vertically in response to crowding (Bertness *et al.* 1998); and, of course, humans construct skyscrapers and basements in crowded cities.

It has been suggested that habitat characteristics such as soil type, depth and vegetation type influence seabird burrow length (Warham 1996, Powell *et al.* 2007). We found that Sooty Shearwater burrows were longer in areas with greater tussac cover. This may be because it is easier to excavate in the peaty soils that accumulate under tussac (Otley *et al.* 2008). This, as well as differences in colony density and therefore competition for space, may explain some of the variability in length of petrel burrows within and between colonies (Table 2). Alternatively, Hamilton (2000) suggested that Sooty Shearwaters may be able to build longer burrows in areas with dense vegetation because soil stability could be greater due the concomitantly deeper and denser root systems. We were unable to measure soil stability in our study, but we saw little evidence of burrow collapse at our study site, suggesting that this may not have affected burrow length. Additionally, there was little support for change in tussac cover influencing burrow length, possibly because peat conditions recovered quickly where tussac cover has increased the most, allowing birds to dig long burrows. Burrow entrance width and entrance

height are likely to be the minimum that allow the passage of a Sooty Shearwater, and therefore are unlikely to vary with habitat. Although we have identified two variables that are likely to be responsible for variability in burrow length, further work is needed to identify other factors which influence burrow dimensions across seabirds.

The potential limiting effect of suitable available nesting habitat, such as tussac grass, has been long recognized in Sooty Shearwaters and other burrowing petrels (Warham 1996). It is possible that there is a positive feedback between Sooty Shearwaters and tussac grass vegetation. Burrowing petrels are known to contribute important nutrients (predominantly guano) to surfaces and burrow systems on islands (Bancroft *et al.* 2005). Vegetation like tussac, with longer roots (Smith & Karlsson 2017) that can reach underground to burrows, are likely to access and benefit from seabird-mediated nutrients, therefore improving vegetation cover and peat depth. Therefore, deposition of nutrients within Sooty Shearwater burrows could support greater tussac cover, which could allow longer burrows to be dug.

Understanding which drivers lead to longer burrows in Sooty Shearwaters can help to inform conservation strategies on islands with burrowing petrel colonies. Our data suggest that shearwater burrows are longer in areas with a higher density of burrows. This suggests that the number of burrows that can be accommodated per unit area can increase if there is sufficient soil depth to allow longer burrows to be constructed. Presumably this is because a greater number of nesting chambers can be accommodated in areas with deeper soils (Ramos *et al.* 1997, Hamilton 2000). In turn, this suggests that soil properties, such as depth and density, may be become limiting as burrow density increases (Hamilton 2000). Soil management could therefore be an important step towards the restoration of shearwater colonies. For example, soils could be improved by restoring tussac grass to areas from which it had formerly been extirpated by humans. Tussac was formerly abundant throughout the coastal margins of the Falklands Islands but was severely depleted due to grazing and fire following human settlement of the archipelago (Strange *et al.* 1988). Such areas tend to have dry, heavily eroded and therefore thin and hard peat soils (Selkirk & Saffigna 1999). In contrast, deep layers of moist and therefore softer peat accumulate beneath healthy tussac. Tussac is now being replanted and protected from grazing in many areas of the Falklands, partially in an attempt to reinstate burrowing seabird populations (Otley *et al.* 2008). According to our relative measure of grass cover based on change in grey raster bands, almost all areas of the island have shown an increase in tussac grass (i.e. there was a near universal increase in 'darkness' of the raster bands). Our study suggests that restoring tussac grass for the benefit of burrowing seabirds may be most effectively accomplished by planting tussac in areas likely to allow deep peat accumulation and, therefore, longer burrow excavation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of model selection results for all candidate and intercept-only models of estimating Sooty Shearwater *Ardenna grisea* burrow entrance width on Kidney Island, Falkland Islands.

Table S2. Summary of model selection results for all candidate and intercept-only models of estimating Sooty Shearwater *Ardenna grisea* burrow entrance height on Kidney Island, Falkland Islands.