Recovery of a sooty shearwater (*Puffinus griseus*) breeding area after habitat destruction

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Abstract: We describe the recovery of an 88-m^2 area of sooty shearwater breeding habitat on Northeast Island, The Snares, New Zealand, during the eight breeding seasons after it was completely destroyed by excavation in December 1996. Burrow entrance density did not differ between the destroyed site and three comparison sites one year after the event. We detected breeding attempts of shearwaters in the season following disturbance, but burrow occupant density recovered more slowly, perhaps because the overall population density was declining over the same period. Burrow occupant density did not differ between the destroyed site and comparison sites within five breeding seasons of disturbance.

Keywords: disturbance; excavation; population recovery

Introduction

In general, the factors limiting seabird populations are poorly understood (Croxall & Rothery 1991), but in some species limitation by territorial behaviour at breeding sites may occur, as has been identified in several other bird groups (e.g. examples in Newton 1992). If present, recovery after disturbance events (such as landslides or trampling) may be influenced by a non-breeding surplus of sexually mature birds. These individuals ('floaters') are prevented from breeding when all potential nesting sites are occupied by territorial resident birds (Manuwal 1974; Newton 1992) and their presence can stabilise populations after perturbations (Sarah et al. 2004). Understanding these dynamics is especially important for species such as Procellariiformes where the implications of disturbance may be profound due to low reproductive output compared with other bird species (Warham 1990), and the possible occurrence of indirect effects of disturbance of breeding attempts, such as the disruption of established pair bonds (i.e. divorce) (Wooller et al. 1988).

We investigated the effects of habitat destruction on the breeding biology of sooty shearwaters (*Puffinus griseus*). We may expect recovery of the site to be rapid if either (1) birds nesting at the site prior to destruction are not unduly disturbed and/or (2) a population of floaters exists that can quickly fill any nesting positions abandoned by resident birds. Recovery will be considerably longer if resident birds abandon the site and there is no floater

population to recolonise it, or if resident or floater birds delay renesting for a long period post-habitat destruction. Additionally, by quantifying the effects of disturbance and recovery to this colony area, we provide an impact assessment of the excavation technique used to assess population monitoring methods. We report the rate of recovery for the destroyed site and compare subsequent habitat changes relative to surrounding breeding habitat during eight consecutive breeding seasons.

Methods

Study site and excavation

Northeast Island, the largest island (280 ha) of The Snares group (48°01′S 166°36′E), had an estimated 2.1 million (95% CI = 1.6–2.6 million) sooty shearwater burrow entrances between 1996 and 2000 with densities >1 m^{-2} in some areas (Scofield 2001). Several well-defined ecotypes are present on Northeast Island. The dominant habitat consists of a closed canopy of the tree *Olearia lyalli* with a notable lack of understorey vegetation due to trampling from sooty shearwater activity and their removal of vegetation for nest material (Fineran 1964). In December 1996, we excavated an 88-m^2 site (hereafter Site C) containing 98 burrow entrances (Hamilton 2000). The excavation coincided with the incubation stage of the annual breeding cycle (which consists of laying of a single egg between mid-November and early December,

hatching in mid–late January, and fledging between late April and early May; Warham 1990). Excavation resulted in the termination of all breeding attempts within the site during that breeding season. We refilled the site with soil in January 1997. Within half of the site we initiated 22 'starter burrows', each 20 cm long, to potentially facilitate recolonisation; no starter burrows were initiated in the remaining half.

Assessing recolonisation

We established three non-destroyed comparison sites randomly within the dominant *Olearia lyalli* ecotype and in reasonably close proximity to the research hut (sites were separated by less than 500 m from each other). We established Site A (501 m², 305 entrances at establishment) at the same time as Site C in December 1996; we established Site B (392 m², 377 entrances) in April 1997 and Site D (628 m², 435 entrances) in January 1998. We monitored sites each breeding season from 1996/97 until 2003/04. The number of visits within each season varied between one and three, coinciding with one or more of three distinct periods of the breeding cycle: the egg stage in December, the hatching/early chick (hatch) stage in January and early February, and the late chick stage in March and April. We performed analyses on data collected only during the hatch periods because effort was most consistent during this period, thus preventing differences in detectability of occupants at different breeding stages from potentially obscuring trends. No data were available for January 1999/2000; therefore, we obtained burrow entrance density for that season in April.

We considered an entrance to be viable if a tunnel extended > 20 cm in length from the entrance, the shortest tunnel length found to be occupied in previous studies

(Lyver et al. 1998). We assessed all viable entrances within the study sites during each visit, using an infrared burrowscope to detect burrow occupants (Lyver et al. 1998).

We calculated burrow entrance density BD (entrances m^{-2}) as $BD = E/A$ where E was the total number of entrances burrowscoped on the site and A the area of the site. Occupancy O (chicks entrance^{-1}) was calculated as $O = C/E$ where C was the total number of chicks or eggs detected on the site. We then calculated occupant densities OD (occupants m^{-2}) at each site as $OD = BD \times O$.

Statistical methods

We assessed recovery by comparing annual rates of change in abundance between Site C and three comparison sites. Because Site C lacked replication, we measured differences by observing whether the rate of change at Site C fell within the (95%) confidence interval spanning the average rate of change for all comparison sites. Because comparison Sites B and D were established in April 1997 and January 1998 respectively, we restricted quantitative comparisons to the period when data from all three comparison sites (i.e. replication) were available. An alpha value of 0.05 was used for all statistical tests and for constructing confidence intervals.

Results

Burrow entrance density

Burrow entrance density in December 1996 was greater at Site C (1.11 m^{-2}) than at Site A (0.61 m^{-2}; Fig. 1). By the end of January 1997, 9 days after Site C was filled-in, shearwaters had excavated 64 burrow entrances (0.73 m^{-2};
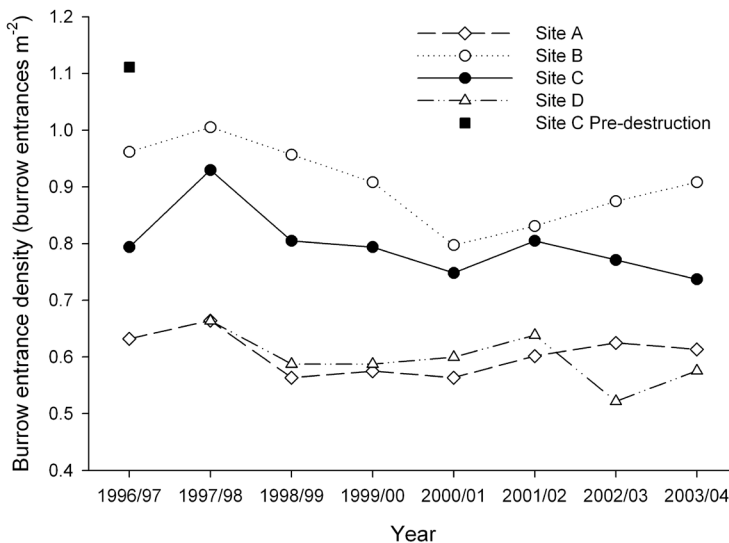

Figure 1. Trends in density of sooty shearwater burrow entrances on Northeast Island, The Snares, between 1996 and 2003 at comparison Sites A, B and D, and the destroyed Site C.

Table 1. Short-term recovery of sooty shearwater burrows at the destroyed Site C in comparison with comparison Site A on Northeast Island, The Snares.

	Burrow entrances	Mean burrow length (cm) ± 95% CI
Site A		
December 1996	305	78 ± 5.8
January 1997	317	86 ± 4.8
April 1997	316	94 ± 5.4
Site C		
December 1996	98	71 ± 14
January 1997	64	79 ± 9.4
April 1997	79	79 ± 9.8

Table 1). Twenty-two of these were the starter burrows provided after filling, all of which had been extended by visiting birds. Seventy-nine burrow entrances (0.90 m^{-2}) were present in April 1997 (Table 1). Burrow entrance numbers at Site A increased slightly from 305 to 317 during the same period. In 1997/98 we recorded the greatest number of burrow entrances at Site C (82 burrow entrances, 0.93 m^{-2}) post-destruction. This was the only season when the (rate of) change in burrow entrance density from the previous season at Site C fell outside the confidence interval observed at the comparison sites (Fig. 2). During the remaining six years, changes in burrow entrance density at Site C were similar to those at the comparison sites. There was little evidence for trends in burrow entrance density, with the slope parameters of linear regressions varying between −0.018 and −0.003, which were not significantly different from zero (all slope

P values > 0.445; autocorrelation r = −0.536 to 0.365, all P values for autocorrelation > 0.215; Fig. 1). During the 8 years following the excavation, burrow entrance density at Site C never reached the density observed before disturbance.

Lengths of burrows where the end of the tunnel was reached were not significantly different between Sites A and C in December 1996 ($t_{2,140}$ = 0.98, P = 0.328; Table 1). Burrows were slightly longer at both sites in January and April 1997 than in December 1996 despite the destruction at Site C and did not differ between sites ($t_{2,197}$ = 1.47, P = 0.143; Table 1).

Occupancy

Before destruction in December 1996, occupancy at Sites A and C was similar (0.65 and 0.69 chicks entrance^{-1} respectively; Fig. 3). Only five breeding attempts were detected in Site C in January of the breeding season following excavation (1997/98; occupancy = 0.06 chicks entrance^{-1}). Initial recovery coincided with substantial decrease in occupancy at Site A between January 1997 and January 1998 (0.57 to 0.14 chicks entrance^{-1}), resulting in the difference in occupancy between the sites being minor in the 1997/98 breeding season. Occupancy during the hatch period at Site C continued to increase slowly until January 2002 with Site A showing a similar pattern (Fig. 3). In January 2002, 5 years after the burrows were destroyed, Site C had a higher occupancy than Site A for the first time post-destruction. This was the only breeding season where the rate of change in occupancy at Site C from the previous season was greater, and fell outside the confidence limits around the mean at the comparison sites (Fig. 4). Site B displayed the highest occupancy of the sites in all years it was monitored (Fig. 3).
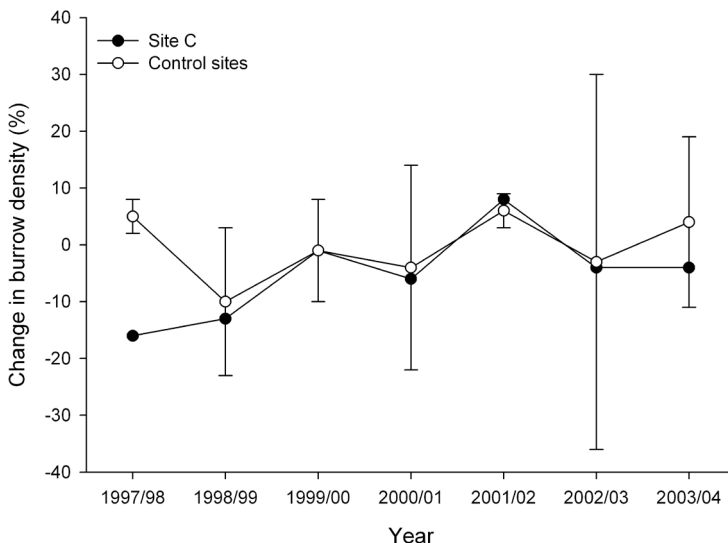

Figure 2. Rate of change in density of sooty shearwater burrow entrances from the preceding breeding season, at destroyed Site C and comparison Sites A, B and D, on Northeast Island, The Snares. Error bars represent 95% confidence intervals.
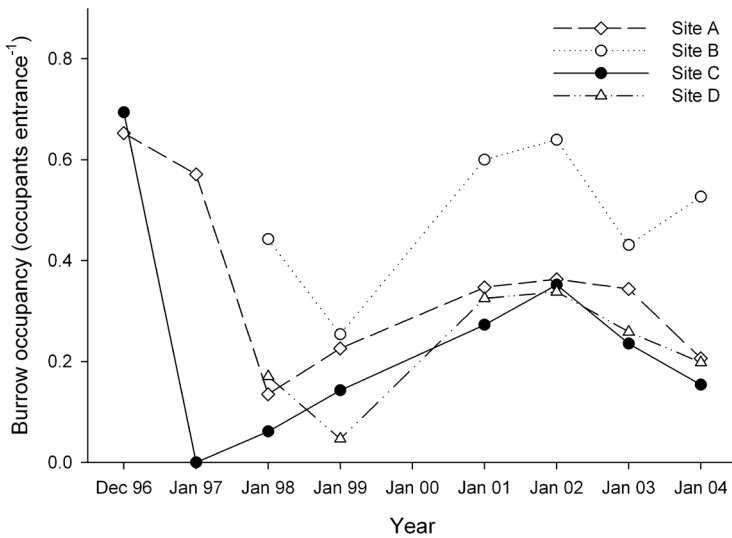
Figure 3. Occupancy of sooty shearwater burrows during January at Northeast Island, The Snares, between 1997 and 2004 at the destroyed Site C and comparison Sites A, B and D. Pre-destruction densities in December 1996 were only available for Sites A and C.
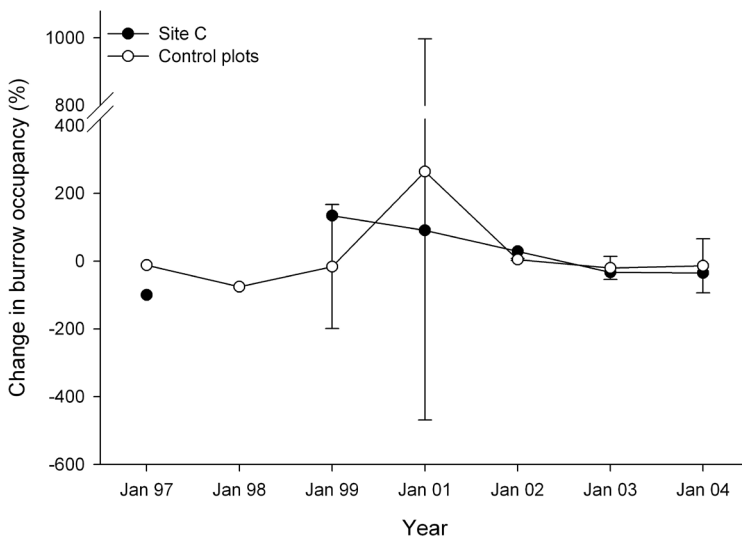

Figure 4. Rate of change in occupancy of sooty shearwater burrows from the preceding breeding season, at destroyed Site C and comparison Sites A, B and D, on Northeast Island, The Snares. Error bars represent 95% confidence intervals. We were unable to calculate the rate of change for Site C in January 1998 as occupancy in the preceding year was zero. The error bar in January 2002 is too narrow to be visible.

Occupant density

Because occupant density is closely related to burrow occupancy we noted very similar trends between these measures. Compared with the previous breeding season, rates of change in occupant density were greater and outside the 95% confidence limits of mean rate of change at the comparison sites in January 1999 and again in January 2002. There was no evidence of further increases in occupant density at Site C after January 2002, with rate of change in occupant density at Site C similar to the comparison sites. In every breeding season that Site B was monitored it exhibited the highest occupant density.

Influence of 'starter burrows'

Nine days after excavation, burrow numbers in the half of Site C where we provided starter burrows were already similar to those in the unmodified half ($\chi^2 = 0.500$, $P = 0.480$; Table 2), with numbers remaining relatively similar for the rest of the monitoring period (Table 2).

Table 2. Percentage of sooty shearwater burrow entrances present in the half of the destroyed Site C with starter burrows provided compared with the half without provision, over time after disturbance, on Northeast Island, The Snares. Statistical tests performed were chi-squared tests of independence.

	January 1997	April 1997	January 2002	January 2004
Starter burrows	56%	53%	45%	54%
No starter burrows	44%	47%	55%	46%
Total	64	79	71	75
χ^2	0.500	0.158	0.345	0.327
P	0.480	0.691	0.557	0.567

Discussion

Recovery of sooty shearwater burrows at an experimentally destroyed site at The Snares was rapid. Burrow entrance density at the destroyed site was greater than that at a nearby comparison site by the end of the 1996/97 breeding season, four months after excavation, and the absence of a continued increase in burrow entrance density relative to comparison sites beyond the season following destruction (1997/98) indicates that as much recovery of burrow entrance density as would occur over the monitoring period was completed after just one year.

Rapid renesting of several birds in the season following disturbance suggests either less time is needed to prepare burrows for nesting than previously thought (Warham 1990), or the birds re-nesting may have 'skipped' breeding (Bradley et al. 2000) in the year of destruction and quickly adapted to the new burrow structures. However, burrow entrance density and occupancy, and thus occupant density, at Sites A and C never reached the levels observed pre-destruction in December 1996. Monitoring of recovery was confounded to a degree by a large decline in occupancy at comparison sites. These declines make it difficult to predict whether recovery of occupant density at Site C would still have reached similar levels to the other sites quickly, or whether recovery would have occurred more slowly.

We attribute some of the observed differences in absolute abundance measures, post-destruction, to the stages of the breeding season being compared. Whereas pre-destruction assessment was during the early incubation period, all post-destruction monitoring occurred during the hatching/early-chick period, after the majority of breeding failure in petrel species is thought to occur (Warham 1990), resulting in lower abundance estimates. The mean decrease in occupancy between incubation and hatching/early-chick monitoring checks, within years, over the four sites was 25%, although this decrease was highly variable (SD = 23%, *n* =8). Applying this mean correction to the highest occupancies observed at Sites A and C during the hatching/early-chick period (both in January 2002) results in occupancies of 0.48 and 0.47

chicks entrance^{-1} respectively, well below the values observed in December 1996 (0.65 and 0.69 respectively). However, the very high variation in the correction results in upper 95% prediction limits of 1.18 and 1.16 respectively. Clearly, making inferences about whether total recovery of density has been achieved is difficult with these data. It is important to note that burrow entrance density also failed to reach pre-destruction levels despite this measure being largely invariant to timing of monitoring.

Ideally, assessing the relative recovery of the site would also have involved regular monitoring during the egg stage; however, monitoring was designed to meet the goals of a wider study. By monitoring the sites during the hatching period, more noise is added to the time-series due to site-specific levels of breeding failure, potentially obscuring differences between sites and affecting our ability to assess recovery. The highly synchronised fluctuations in abundance observed between the sites would be very unlikely in the presence of such site-specific differences in breeding success, suggesting that in this case confounding of relative recovery has probably not occurred.

The failure of breeding and habitat parameters to recover to pre-destruction levels may be related to the 37.3% decline in burrow entrance density of sooty shearwaters at The Snares between 1969–1971 and 1996–2000 (Scofield 2001). Although measurement of changes in burrow occupancy in that study were unreliable, any decline continuing over our monitoring period may explain part of the failure to fully recover. Alternatively it is possible that occupant density in the 1996/97 breeding season was particularly high, as temporal variation in the proportion of sexually mature individuals breeding is a common feature of long-lived seabirds (Dunlop et al. 2002).

Uncertainty in the origin of individuals recolonising the site restricts our inferences to identifying a lack of a non-breeding surplus, which would be evidenced by very slow recovery of the site. The only experimental evidence demonstrating territorial limitation in seabirds that we are aware of is a study of Cassin's auklets (Manuwal 1974). In that study, removal experiments identified a sizable surplus

of sexually mature individuals that quickly occupied sites vacated by removed birds, indicating limitation through territorial behaviour. As recovery in our study appeared to be fairly rapid we are unable to rule out the possibility of breeding sites limiting the sooty shearwater population at The Snares. We suggest that either birds previously breeding at the site were not unduly disturbed and quickly recolonised the site and/or new recruits (those just attaining breeding status and/or floaters) quickly filled vacant nesting sites. Recent declines of sooty shearwaters on The Snares (Scofield 2001) and elsewhere (Lyver et al. 1999) suggest that populations may be reduced below levels where territorial limitation may be expected to occur, supporting the former hypothesis.

Conclusions

Recovery of Site C appeared to be relatively rapid with effects appearing to be restricted to a short-term reduction in breeding productivity, although uncertainties of whether the site fully recovered remain. Small-scale, short-duration disturbance events where impacts are restricted to fecundity (to which growth rate of sooty shearwaters is largely insensitive; Hunter et al. 2000), such as occurred here, therefore appear to be relatively minimal at the colony or population level for sooty shearwaters. Starter burrows appear to have limited utility in stimulating colony recovery when the substrate is friable and the species displays good burrowing ability.

Acknowledgements

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