BURROW ENTRANCE ATTRITION RATE IN WEDGE-TAILED SHEARWATER *PUFFINUS PACIFICUS* COLONIES ON ROTTNEST ISLAND, WESTERN AUSTRALIA

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SUMMARY

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Shearwaters (*Puffinus* spp.) appear to select burrow-nest sites to minimise the risk of burrow collapse and are known to clear and re-excavate damaged burrows, yet empirical evidence on the incidence of burrow collapse is lacking. We provide preliminary data on rates of burrow entrance collapse in a colony of Wedge-tailed Shearwaters (*P. pacificus*) on Rottnest Island, Western Australia. Entrances to 67.8% of burrows that were active during the laying phase of the 2002/03 breeding season had collapsed by the beginning of the next season. The attrition rate was linear over time, and collapsed portions had a mean length of 17.9 ± 2.7 cm (standard error). Burrow entrances overlain with shallow-rooted, annual plants (89.7% collapse rate) were more than twice as likely to collapse as those located beneath deeper-rooting, perennial shrubs (40.9% collapse rate). Three quarters of collapsed entrances were re-excavated the following season, and at least 11.5 t ha^{-1} yr^{-1} (8.5 m^3 ha^{-1} yr^{-1}) of soil was displaced through this process. Of marker posts that were placed at the entrances of burrows in 1992 (n = 264), 22% were found in 2003. Of the posts that were found, 19% remained associated with a burrow entrance. We consider that most entrance collapses in this study reflect abandonment of burrows by the birds. Our data predict that, if a current increase in shallow-rooted vegetation in colony areas continues, the rate of entrance collapse and colony erosion will increase. Although we did not attempt to quantify the effect that burrow entrance collapse has on the reproductive biology of the shearwaters, we hope that our work will catalyse future investigation in this field.

Key words: Shearwater, burrow, collapse, biopedturbation, ecosystem engineering, Rottnest Island

INTRODUCTION

Shearwaters *Puffinus* spp. are gregarious, pelagic seabirds that breed monogamously and show a high level of mate fidelity (Warham 1990). The birds are colonial nesters, usually on islands, and almost all species excavate burrows in which a single egg is incubated per year. The chick remains in the burrow until fledging. Burrows convey a range of advantages to shearwaters, such as shelter from environmental extremes or aerial predators, amplification of vocal communication, and constant atmospheric conditions and associated physiologic benefits (Whittow *et al.* 1987, Warham 1990, Johnstone & Storr 1998). Colonies, however, are often positioned in exposed areas where the prevailing weather can cause erosion or damage to burrows that is disadvantageous to the occupants (Warham 1990, Furness 1991). The most commonly cited problem is inundation of burrows with water, from heavy rainfall events or high tides, and subsequent nest failure (e.g. Brooke 1990, Warham 1990, Thompson & Furness 1991, Brown *et al.* 1993, Schreiber & Burger 2002). Where rainfall and tides do not exert a major influence, the physical collapse of burrows may be an important determinant of reproductive success (Harris 1984, Carter 1997).

Although it is generally accepted that shearwaters select nest sites so as to minimise the risk of burrow collapse and that soil strength, soil moisture content and overlaying vegetation may affect the burrow integrity, published information on the frequency of burrow collapse is lacking (Neil & Dyer 1992, Carter 1997). Similarly, all ecologic summaries of shearwater reproductive biology indicate that at least some birds will re-excavate partially collapsed burrows at the commencement of a breeding season, yet scant empirical evidence is available about the extent of this behaviour (Marchant & Higgins 1990, Warham 1990, Schreiber & Burger 2002).

Here we report the results from a small experiment that investigated the attrition rate of burrow entrances in a colony of Wedge-tailed Shearwaters *P. pacificus* on Rottnest Island, Western Australia. We present data on the natural rate of burrow entrance collapse over a single breeding season and the subsequent winter, the proportion of collapsed-entrance burrows that are re-excavated at the beginning of a breeding season, the effect of overlaying vegetation type, and the proportion of burrows that have persisted over a 10-year period. We use our data to calculate the soil displacement rate associated with burrow entrance re-excavation, and we make suggestions on future research directions and considerations.

METHODS

Site and shearwater breeding phenology

The study was conducted on Rottnest Island (32°00′S, 115°31′E), 18 km off the coast of Fremantle, Western Australia. The two largest colonies on the island were the sites for the study: Radar Reef colony for re-excavation rate, natural decay and long-term burrow persistence studies, and Cape Vlamingh for the natural decay study. For colony maps and descriptions see Bancroft *et al.* (2004a).

The breeding phenology of Wedge-tailed Shearwaters on Rottnest Island has been documented by Marchant & Higgins (1990), Garkaklis *et al.* (1998) and Johnstone & Storr (1998). Adult birds arrive in mid-August to begin burrow excavation or clearing and courting, with a two-week pre-laying exodus occurring in early November. Eggs are laid and incubated from late November. Chicks hatch from mid-January, are reared from January to late April, and fledge by mid-May. Birds migrate away from the island for the remainder of the year.

Re-excavation rate

The re-excavation rate study commenced in July 2002, during the period when the shearwaters were absent from their breeding colonies. We selected 20 burrows through randomly generated compass bearings and distance measurements from an arbitrarily placed origin within the colony. At each burrow, the entrance and the first 30 cm of tunnel were manually collapsed, and the area was levelled flush with the surrounding colony surface. Burrows were subsequently examined on seven occasions between 3 September 2002 and 13 May 2003, and scored as open (entrance clearly re-excavated and birds in occupation) or collapsed (entrance collapsed and no evidence of occupation).

Natural decay

The rate of natural burrow decay was measured by marking 90 active burrows during the laying phase of the shearwaters' breeding cycle (see Bancroft *et al.* 2005a) to ensure that all were well-established burrows (18 December 2002). Burrows were categorised as "active" if fresh tracks or diggings or both were consistently observed at the entrance in the two weeks before commencement of the study. Burrows were chosen at random as described for re-excavation rate. The plant species overlaying the entrance to each burrow were recorded. Burrows were inspected on four occasions until just before the subsequent breeding season (19 August 2003) and were scored as "open" (entrance relatively clear of soil) or "collapsed" (entrance blocked by soil or no longer existent). It is not thought that Wedge-tailed Shearwaters actively plug their burrow entrances (Marchant & Higgins 1990). Where the entrance was blocked, an estimate of the length of the collapsed portion of the burrow was made.

An estimate of the rate of soil disturbance attributable to burrow entrance collapse was made with reference to the calculations of Bancroft *et al.* (2004b). The mean cross-sectional area of a burrow (Bancroft *et al.* 2004b) was multiplied by the mean length of entrance collapse, derived here, to estimate mean collapse volume. This figure was then multiplied by mean burrow density (Bancroft *et al.* 2004a) to estimate mean volume of collapse per unit of colony area. That result was further multiplied by mean soil bulk density (Bancroft *et al.* 2004b) to estimate the mass of soil displaced through collapse per unit area.

Long-term burrow persistence

In 1991/92, 264 burrows at Radar Reef were marked during a study of shearwater breeding phenology (Garkaklis 1992, Garkaklis *et al.* 1998). A search and count of these posts was made in February 2003, and we recorded whether each post was convincingly associated with a burrow entrance (within 30 cm).

RESULTS

Three quarters of burrow entrances that were collapsed during the non-breeding season were re-excavated once shearwaters returned to their colonies (Table 1). Most of these burrows had been re-excavated by mid-October, with the peak in December. A decrease from December to May represents natural attrition. Once a burrow entrance had re-collapsed (within the breeding season), it was not re-excavated.

Of burrows active during the laying phase of one season, only 32.2% remained open before the commencement of the next season (Fig. 1). We observed a significant, negative, linear regression between the day of observation and the percentage of burrows that remained open (Fig. 1; $y = -0.286x + 96.997$; $R_a^2 = 0.956$; ANOVA: $F^{1,3} = 87.1$, $P = 0.003$). A greater proportion of burrow entrances that were overlain with the prostrate annual plant *Mesembryanthemum crystallinum* had collapsed by the end of the study (89.7%) than had entrances located under at least one species of perennial shrub (40.9%; *Rhagodia baccata, Tetragonia implexicoma* or *Threlkeldia diffusa*; Table 2). On average, 17.9 ± 2.7 cm (standard error; range: 5–105 cm) of the burrow entrance had collapsed.

TABLE 1
The percentage of experimentally collapsed Wedge-tailed Shearwater *Puffinus pacificus* burrows that had been re-excavated on each of the occasions surveyed

Date	Open burrows (%)
31 July 2002	0 [a]
3 September 2002	45
6 September 2002	60
23 September 2002	60
12 October 2002	65
17 December 2002	75
19 February 2003	75
13 May 2003	45

[a] All burrows were experimentally collapsed on this date.

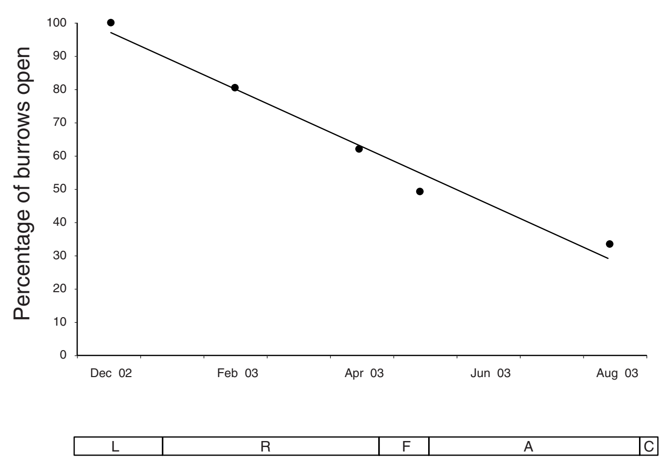

Fig. 1. Linear regression of the percentage of burrows that remained open throughout the study. See text for regression equation. Breeding phases are shown below chart and follow Bancroft *et al.* (2005): L, laying; R, rearing; F, fledging; A, absent; C, clearing.

Given the mean burrow dimensions, shape, burrow density and soil bulk density on Rottnest Island (Bancroft *et al.* 2004a, 2004b), and the mean length of entrance collapse reported here, at least 11.5 t ha^{-1} yr^{-1} (8.5 m^3 ha^{-1} yr^{-1}) of soil is displaced through clearing of burrow entrances.

Of 264 marker posts placed in the shearwater colony by Garkaklis (1992), 59 were found (22%). Eleven of these (19% of posts found, 4% overall) were still associated with a burrow.

DISCUSSION

Quantitative studies of burrow collapse rate are rare. This rarity could be a function of the difficulty in defining a burrow collapse. We circumvented the problem by restricting our definition to the collapse and blockage of burrow entrances. However, in the absence of burrow occupancy data, it is difficult to assess the ecologic meaning of entrance collapse.

We previously showed that, when present, birds continually eject soil from their burrows throughout the breeding season (Bancroft *et al.* 2005a). Given the high rate of re-opening of collapsed entrances at the beginning of a breeding season, it seems unlikely that mid-season collapse would prohibit further attendance by shearwaters. Collapse of entrances within a breeding season most likely reflects abandoned burrows and is only recorded when birds are no longer maintaining the burrow. The 2002/03 breeding season was poor for Wedge-tailed Shearwaters, with a relatively low level of burrow occupancy on many Western Australian islands (I. Kirsten, C. Surman & N. Dunlop pers. comm.), and may explain the high rate of attrition observed here. Level of occupancy must be taken into consideration in future studies of burrow entrance attrition rate.

Burrow entrances dug beneath the shallow-rooted, annual *M. crystallinum* were more than twice as likely to collapse as those under deeper-rooting, perennial shrubs. Although roots may make burrow construction more difficult for the shearwaters, they also stabilise the soil, preserve burrow integrity and reduce the volume of soil excavated (Gillham 1961, Harris 1984, Warham 1990). Burrowing by shearwaters on Rottnest Island promotes annual, shallow-rooted vegetation (Bancroft *et al.* 2005b), and in the last 50 years, the colonies have also dramatically expanded in size (Bancroft *et al.* 2004a). If these trends continue, our data predict an increase in the rate of entrance collapse, an increase in soil displacement, and an increase in the erosion of colony areas.

Long-term persistence of burrows is a complex and debateable issue. There is no doubt that seabird burrows are dynamic in shape, structure, location and persistence (Harris 1984, Bancroft *et al.* 2004b). We found only 22% of 264 marker posts that were placed beside burrow entrances a decade earlier. Of those posts, 19% (4% overall) were clearly associated with a burrow entrance in 2003. Therefore, because we could not determine the fate of a large proportion of the undetected original markers, we estimate that 4%–19% of Rottnest Island burrows maintained integrity over a decade. We acknowledge that our estimate probably carries a high degree of error, but we consider it a first attempt at tackling a long-avoided question. It is convenient and practical to mark burrows at their entrance; however, we saw that burrows can shorten by up to 105 cm within a single season. Therefore, although a burrow entrance is no longer obviously associated with a marker, that lack of association does not necessarily mean that that burrow has been completely destroyed or has lost its function. Given the burrow-fidelity reported by many authors (e.g. Serventy *et al.* 1971, Brooke 1990, Marchant & Higgins 1990, Warham 1990, Schreiber & Burger 2002), perhaps occupants could be used to identify burrows, rather than vice versa. Frequent burrow inspections (e.g. weekly to monthly, rather than yearly as in some studies [Bradley *et al.* 2000]) would almost certainly identify recent collapses.

TABLE 2
The number and percentage of collapsed Wedge-tailed Shearwater *Puffinus pacificus* burrows that were overlain by *Mesembryanthemum crystallinum* only, or by at least one of the shrubs *Rhagodia baccata, Tetragonia implexicoma* or *Threlkeldia diffusa*

Plant species	Open on 18 December 2002 (n)	Collapsed by 19 August 2003 (n)	% Collapsed
Mesembryanthemum crystallinum only	68	61	89.7
At least one shrub	22	9	40.9

Navigation to individual nesting burrows by seabirds has been subject to conjecture. Several mechanisms have been proposed, including ultrasonic, mate-to-mate auditory, visual and olfactory cues, and memory (Serventy *et al.* 1971, Furness 1991). Serventy *et al.* (1971) argue that a combination of sight and memory is used. Birds were able to locate and re-excavate three quarters of entrances that, to the human eye, were compacted and levelled flush with the adjacent ground surface. Vegetation cover also dramatically changed between breeding seasons (Bancroft *et al.* 2005b), with many former burrow entrances grown over. In no instance did we find evidence of any exploratory digging near the burrow entrances.

Although our results do not provide an indication of the effect of burrow entrance collapse on the reproductive biology of the Wedge-tailed Shearwater, they supplement our previous investigation of biopedturbation (digging and burrowing [Bancroft *et al.* 2004b]) and contribute to an appreciation of these birds as "ecosystem engineers" (Jones *et al.* 1994). Approximately 51% of all burrow entrances would have collapsed and been reopened between breeding seasons. Burrow entrance collapse was estimated to displace at least 11.5 t ha^{-1} yr^{-1} (8.5 m^3 ha^{-1} yr^{-1}) of soil. Summed with our previous estimates of annual soil displacement (derived from colony expansion data and not re-excavation, [Bancroft *et al.* 2004b]), this equates to at least 22.0 t ha^{-1} yr^{-1} (16.3 m^3 ha^{-1} yr^{-1}). This figure does not include soil excavated from burrow extension or internal burrow collapse and is likely to be an underestimate of the actual biopedturbation rate.

The effect of the physical environment—and burrow decay—on the reproductive success and mortality of shearwaters remains unclear. However, we have made a first attempt to quantify the dynamic nature of seabird burrows. Clearly burrow entrance collapse is a major driver of soil displacement by these animals, and it affects most burrows. Although we have reported only simple attrition rates and cannot predict whether entrance collapse promotes or follows burrow abandonment, our data will hopefully catalyse further investigation into the association of burrow entrance collapse with the reproductive success of burrowing seabirds.

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