NEAREST NEIGHBOUR ANALYSIS AND SPATIAL RELATIONSHIPS OF WEDGE-TAILED SHEARWATER, *PUFFINUS PACIFICUS,* (AVES: PROCELLARIIFORMES) BURROW ENTRANCES AT RADAR REEF, ROTTNEST ISLAND, WESTERN AUSTRALIA

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(with one text-figure and one table)

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The spatial distribution of Wedge-tailed Shearwater burrow entrances on Rottnest Island, Western Australia, was investigated using the single- and two-sector nearest neighbour methods of point pattern analysis. Both analyses yielded similar results. Mean burrow density was 0.32 ±0.02 SE burrows m^{-2}, burrow entrances were not distributed at random and entrances tended towards an even distribution. Evenness of distribution was positively correlated with burrow density. Social and structural factors are likely to be important in determining burrow entrance distribution by Wedge-tailed Shearwaters and there appears to be a density-dependent trade-off between social benefit (aggregated burrow entrances at low densities) and colony stability (evenly distributed burrow entrances at high densities).

Key Words: Shearwater, burrow, nearest neighbour analysis, Procellariiformes, Rottnest Island, burrow density.

INTRODUCTION

Burrow-nesting is common among seabirds of the Procellariiformes (Furness 1991). Benefits of burrowing include shelter from environmental extremes or predation, amplification of vocal signals and physiological advantages of a more stable microclimate (Whittow *et al.* 1987, Warham 1990). Burrowing may, however, destabilise the soil and lead to burrow collapse or erosion of colonies which can reduce breeding success through direct mortality or the loss of breeding sites (Furness 1991, Bancroft *et al.* 2005).

The spatial distribution of procellariiform burrows within a colony may influence the risk of burrow collapse or erosion. Given an homogenous environment, and on the basis of structural stability alone, an even distribution of burrows within a colony would be expected (Butler 1995): the further the burrow entrances are from one another, the less likely they are to collapse (through increased communal traffic near the entrance or by a reduction in the soil supporting the burrow roof). However, other factors such as soil strength (Neil & Dyer 1992), ground debris (Hill & Barnes 1989), vegetation type (Floyd & Swanson 1983, Hill & Barnes 1989) and social interactions or relationships (Dyer & Hill 1990) may also influence the location and distribution of burrows within a colony.

A convenient method for examining the spatial distribution of burrows is the nearest neighbour method of point pattern analysis (Taylor 1977). Nearest neighbour analysis compares the observed mean nearest neighbour distance to an expected mean, under the Poisson distribution, to produce a divergence from randomness value, R (Taylor 1977). The divergence from randomness provides a measure of the aggregated (low R), random (moderate R) or even (high R) nature of the spatial distribution of points.

Two studies have used nearest neighbour analysis to investigate the spatial distribution of burrow entrances within Wedge-tailed Shearwater, *Puffinus pacificus* (J.F. Gmelin, 1789), colonies (Dyer & Hill 1990, 1995). These studies identified contrasting patterns in the distribution of burrow entrances. Dyer & Hill (1990) found burrow entrances were moderately aggregated but burrows tended towards an even distribution in the Dyer & Hill (1995) study.

The nearest neighbour analysis is biased towards aggregation when only a single nearest neighbour measurement (single-sector) is taken from each point (Taylor 1977), as was the case in the Dyer & Hill (1990, 1995) studies. Bias can be reduced by averaging the nearest neighbour distances obtained from each of two "hemispheres" surrounding a burrow (a "two-sector" analysis, Taylor 1977).

Dyer & Hill (1990) also found that there was a strong positive correlation between burrow density and evenness of dispersion. Such a correlation could be driven by an attempt to maximise the distance between burrows in order to attain the highest level of structural stability possible (Butler 1995), yet Dyer & Hill (1990, 1995) argued that social interaction was the key factor in determining where birds position their burrows.

Here I investigated the spatial distribution of Wedge-tailed Shearwater burrow entrances in a colony on Rottnest Island, Western Australia, using a two-sector nearest neighbour analysis. Comparison was made to a single-sector analysis. In addition, Bancroft *et al.* (2004) observed that burrow densities were lower on the edge of the Rottnest Island colonies and hypothesised that position within the colony, and in relation to the edge of the island, affected burrow density. Therefore, the present study also investigated the relationships between burrow distribution, burrow density and the distance of burrows from the edge of the colony and the edge of the island.

METHODS

Study site

The study was conducted on Rottnest Island (32°00'S, 115°31'E), southwestern Western Australia (fig. 1), on 4–24 September 2002. The study site, Radar Reef, is the largest of six colonies on the island (Bancroft *et al.* 2004).

Field methods

Quadrat size may influence nearest neighbour analyses (Dyer & Hill 1990). For consistency, and to facilitate comparison, the 10 m x 3 m quadrats identified as appropriate by Dyer & Hill (1990) were used in this study. Quadrats were located adjacent to one another (end on end) along three systematically spaced transects that ran between the north and south boundaries of the colony.

All burrow entrances within a quadrat were marked, counted and the distance (to the nearest 5 cm) to the nearest neighbouring entrance was measured in two arbitrarily determined sectors: to the south (between compass bearings 90° and 270°), and to the north (between 0° and 90°, and 270° and 360°). Burrow entrances outside the quadrats were used as nearest neighbours, where appropriate, to avoid boundary effects (Dyer & Hill 1990). The location of the centre of each quadrat was recorded using a hand-held GPS.

Data analysis

Analysis of nearest neighbour measurements followed Taylor (1977). The actual mean nearest neighbour distance, r_{ak}, is calculated from the measurements taken from k sectors around each of n points in an area A.

The expected mean nearest neighbour distance, $r_{ek} = \sqrt{k}/2\sqrt{(n/A)}$

The divergence from randomness, $R_k = r_{ak} / r_{ek}$

The maximum theoretical divergence from randomness, $R_{k.max} = 2.1491/\sqrt{k}$

The standard error of r_{ek}, $SEr_{ek} = 0.26136/\sqrt{(n2/A)}$

The z variate, $z_R = | r_{ek} - r_{ak} | / SEr_{ek}$

Point distribution can be assessed by comparing R_k with $R_{k.max}$, and by using the z variate to test whether r_{ak} and r_{ek} are significantly different.

GIS (ArcView, version 3.0) was used to calculate the minimum distance between each burrow and the edge of the colony and the edge of the island. Correlation coefficients were calculated to examine the relationships between distribution, burrow density and the distance of burrows from the edge of colony and the edge of the island (SPSS v11.0.0).

RESULTS

A total of 233 burrows in 24 quadrats were surveyed. The mean burrow density across all quadrats was 0.32 ±0.02 SE burrows m^{-2} (range 0.13–0.60 burrows m^{-2} for individual quadrats).

The mean actual two-sector nearest neighbour distance (r_{a2}) for all quadrats was 1.42 ±0.03 SE m (range 1.19–2.49 m). The expected mean of randomly distributed burrow entrances (r_{e2}) for two sectors and for the mean burrow density observed in this study was 1.24 ±0.03 SE m. The r_{a2} was significantly greater than the r_{e2} ($z_R = 5.90$, $P < 0.0001$), confirming the non-random distribution and tendency towards maximum possible spacing (evenness).

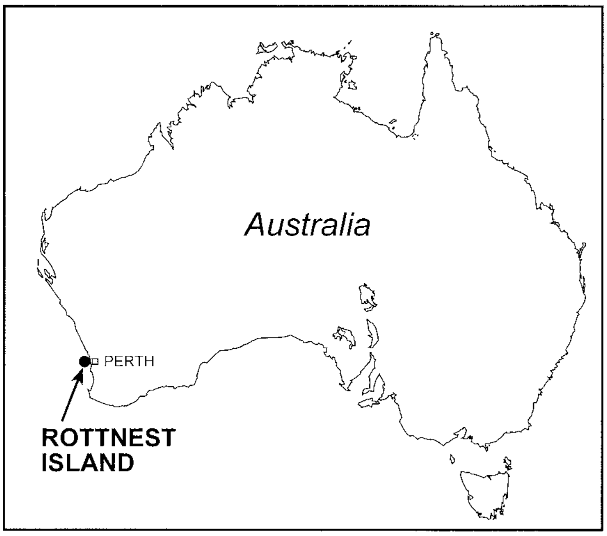

FIG. 1 — Location of Rottnest Island.

The maximum theoretical divergence from randomness for two sectors ($R_{2.max}$), where all burrow entrances are evenly dispersed, is 1.52. The observed R_2 for all quadrats was 1.14 and indicated a tendency towards an even distribution of entrances (range 0.91–1.44 m for individual quadrats).

The minimum nearest neighbour distances for each burrow were used to repeat the analysis using only one measurement per burrow (single-sector) and facilitated a comparison of the outcomes of both a single- and two-sector analysis of the same data. Both analyses indicated the same trend in burrow distribution. The r_{a1} (1.08 ±0.03 SE m) was significantly greater than the r_{e1} (0.88 ±0.03 SE m; $z_R = 6.62$, $P < 0.0001$), suggesting evenness of dispersion. Similarly, the observed R_1 for the single-sector analysis ($R_1 = 1.23$) tended towards the maximum possible ($R_{1.max} = 2.15$), although not as convincingly as the two-sector analysis.

The correlation coefficients between burrow density, two-sector divergence from randomness (R_2), distance to the edge of the colony, and distance to the edge of the island are presented in table 1 (the correlation between distance to edge of colony and distance to edge of island has little meaning and was not calculated). The only significant correlation was that between burrow density and R_2 ($r = 0.42$, $P = 0.04$), indicating that burrow entrances are more evenly dispersed at higher densities. All other correlations were not significantly different from zero; there was no linear relationship between the distance to the edge of the colony or the distance to the edge of the island and either dispersion of burrows or burrow density.

DISCUSSION

The spatial distribution of Wedge-tailed Shearwater burrow entrances within the Radar Reef colony on Rottnest Island was non-random and tended towards evenness. The same result was obtained from both single- and two-sector nearest neighbour analyses of the data, and, therefore, the results are comparable with the single-sector analyses of Dyer & Hill (1990, 1995).

TABLE 1
Correlation coefficients between spatial properties of Wedge-tailed Shearwater burrows at Radar Reef, Rottnest Island

	Burrow density	Two-sector divergence from randomness (R_2)
Distance to edge of colony	−0.19 (P = 0.378)	0.12 (P = 0.592)
Distance to edge of island	0.11 (P = 0.609)	0.08 (P = 0.717)
Two-sector divergence from randomness (R_2)	0.42 (P = 0.040)	–

Probabilities in parentheses. N = 233 burrows (in 24 quadrats). Note that rhe correlation between distance to edge of colony and distance to edge of island was not calculated.

Dyer & Hill (1990) implicated social relationships as the cause of burrow entrance aggregation in Wedge-tailed Shearwater colonies on Heron and Masthead islands. They suggested that shearwaters actively positioned their burrows near to one another to facilitate vocal communication and social interaction, and that, in some cases, offspring may choose to construct burrows in close proximity to their own parents. Dyer & Hill (1990) did not consider that structural stability of the colonies was an influential factor. A colony of much higher burrow density (more than fourfold) on North Stradbroke Island was examined and revealed a more even distribution of burrow entrances (Dyer & Hill 1995), as was observed at Radar Reef in this study, yet the authors maintained that structural stability was not a causal factor. Instead they offered an alternative explanation based on social behaviour. They argued that because the North Stradbroke colony was only 12 years old, the social interactions that drive clustering of burrow entrances (as suggested by Dyer & Hill 1990) had not had time to develop.

The Wedge-tailed Shearwater colony at Radar Reef has been present since at least the 1950s (Saunders & de Rebeira 1993), yet it still demonstrated a tendency towards evenness of burrow entrance distribution. It had a similar mean burrow density to that of North Stradbroke Island (when studied by Dyer & Hill 1995) and more than three times that of Heron and Masthead islands (when studied by Dyer & Hill 1990). I consider that burrow entrance distribution is more likely to be structurally, rather than socially, driven on Rottnest Island. From a structural perspective, the even distribution of burrow entrances is likely to be the most stable and would reduce the instances of burrow entrance collapse and erosion (Butler 1995, Bancroft *et al.* 2005). Other potential physical drivers of burrow distribution (e.g., soil strength, ground debris and vegetation type) were not measured in this study; however, given the even distribution of burrows at Radar Reef, these are likely to either be homogenous throughout the colony or insignificant in their influence on burrow distribution.

A significant positive correlation was observed between burrow density and the divergence from randomness of their distribution (R_2) within the Radar Reef colony. Burrow entrances in areas of higher density are more evenly distributed, a confirmation of the finding of Dyer & Hill (1990). By definition, burrows will be closer at higher densities. In this situation burrowing further (than random) from a neighbour, in an even pattern, has a selective advantage because it is likely to improve burrow entrance stability and avoid burrow collapse that may result in reduced reproductive success (through adult, chick or egg mortality, or the degradation of a suitable breeding site). Ramos *et al.* (1997) found that shorter nearest neighbour distance (between burrow entrances) had a negative impact on the hatching success in Band-rumped Storm Petrels, *Oceanodroma castro* (Harcourt, 1851), but no effect in Cory's Shearwaters, *Calonectris diomedea* (Scopoli, 1769). The potential mechanisms of the impact were not discussed by Ramos *et al.* (1997). Empirical evidence as to the structural stability of aggregated or evenly dispersed burrow entrances is not available. A comprehensive study that examines physical colony characteristics, social relationship, burrow stability and reproductive success, simultaneously, would clarify these issues.

When considered with the findings of Dyer & Hill (1990, 1995), the results from Radar Reef suggest that there is a density-dependent trade-off between social benefit (aggregated burrow entrances) and colony stability (evenly distributed burrows). It appears that at lower burrow densities (e.g., less than 0.1 burrows m^{-2}; Dyer & Hill 1990) Wedge-tailed Shearwaters favour an aggregated distribution of burrow entrances that may reflect social interactions. At higher densities (greater than 0.3 burrows m^{-2}; Dyer & Hill 1995, this study), the birds construct their burrow entrances in a more even distribution that, most likely, reflects attempts to maintain the structural stability of the colony.

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