



Burrow building in seabird colonies: a soil-forming process in island ecosystems

Wesley J. Bancroft^{a,*}, Mark J. Garkaklis^{b,c}, J. Dale Roberts^a

^aSchool of Animal Biology, M092, University of Western Australia, Crawley, WA 6009, Australia

^bWestern Australian Department of Conservation and Land Management, Swan Region, PO Box 1167, Bentley Delivery Centre, Bentley, WA 6983, Australia

^cSchool of Biological Sciences and Biotechnology, Murdoch University, Murdoch, WA 6150, Australia

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Summary

Soil modification via biopedturbation by burrow-building seabirds was examined in a Mediterranean, island ecosystem. Physical and chemical soil properties were compared between a colony of Wedge-tailed Shearwaters (*Puffinus pacificus*) and adjacent heath across a 14-month period. When compared to heath soil, the biopedturbated soil was 28% drier (6.04 ± 5.40 vol%), had increased bulk density (by 29% to 1.30 ± 0.11 g cm⁻³, 51% porosity), wetting capacity (by 83% to 0.55 ± 0.83 molarity of ethanol droplet), hydraulic conductivity (by 266% to 398.91 ± 252.04 mm h⁻¹), and a greater range in soil surface temperature (31.7 ± 6.2 °C diurnally to 18.3 ± 3.2 °C nocturnally). Soil penetration resistance was reduced by 26% at a depth of 0–100 mm (326.5 ± 122.4 kPa) and by 55% at 500–600 mm (1116.8 ± 465.0 kPa). Colony soil also had increased levels of nitrate (by 470%), phosphorous (118%), ammonium (102%), sulphur (69%), and potassium (34%), decreased levels of iron (by 50%) and organic carbon (61%), was more alkaline, and had a 78% greater conductivity. Shearwaters deposited guano at a rate of 234.4 kg ha⁻¹ yr⁻¹ (dry mass). Chemical analysis of guano equated this to 50.9, 5.7, 5.5, and 3.6 kg ha⁻¹ yr⁻¹ of nitrogen, potassium, sulphur, and phosphorous, respectively. Experimentally constructed burrows demonstrated that digging alone can alter physical and chemical soil factors, but that changes in the nutrient profile of colony soils are predominantly guano-driven. We argue that the physical impact of seabirds on soil should not be overlooked as a soil-forming and ecosystem-shaping factor in island ecosystems, and that biopedturbation can exert major bottom-up influences on insular plant and animal communities.

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*Corresponding author. Tel.: +61 8 6488 1493; fax: +61 8 6488 1029.

E-mail address: wes@graduate.uwa.edu.au (W.J. Bancroft).

Introduction

Ecosystem processes are defined as the transfer of energy or matter between components of the system, and it is these processes that regulate the structure of the system as a whole (Chapin et al., 2002). Soil properties are a major factor that govern ecosystem processes and can have a major impact on ecosystem function (Chapin et al., 2002). Soil properties may be influenced by a range of factors including the nature of the parent material, climate, topography, time, and the biota (Murphy, 2000). Until recently the role of vertebrates in governing soil properties was viewed as a small-scale disturbance in the landscape (Butler, 1995), but several studies have now shown that even localised soil disturbance events by fauna may contribute significantly to habitat heterogeneity at the landscape scale (for reviews see Kinlaw, 1999; Whitford and Kay, 1999). In particular, vertebrate biopedturbation, the disturbance of soil by vertebrate animals, has been implicated in structuring ecosystems and ecosystem function (Butler, 1995; Whitford and Kay, 1999). For example, the burrows or diggings of a range of mammals have been shown to change soil bulk density, water infiltration, pH, organic matter or nutrient content, which has led to changes in surrounding plant communities (Reichman and Smith, 1990; Kinlaw, 1999; Whitford and Kay, 1999).

Vertebrate biopedturbation has received most attention from mammalogists studying desert systems in Africa and America (see reviews by Reichman and Smith, 1990; Kinlaw, 1999; Whitford and Kay, 1999), yet it may be an ecologically significant modifier of ecosystem function in all environments (Butler, 1995). The role of biopedturbation in island ecosystems has received relatively little attention (Gillham, 1956; Butler, 1995). Islands are useful models because they are geographically well defined, self-maintaining, and often house the fundamental processes of continental systems in a simplified manner (Vitousek et al., 1995). For island ecosystems it is likely that soil processes are a particularly critical functional element for several reasons: aggregation of soil is poor, nutrient composition of soil is poor, soils have a high water infiltration rate, harsh environmental conditions prevail (e.g. salinity, winds), habitat is often unique and fragile, and island communities often exist in an unstable state of equilibrium (Millar et al., 1965; MacArthur and Wilson, 1967; Miller, 1977; Hasset and Banwart, 1992; Rippey and Rowland, 1995). Island ecosystems are also often of considerable conservation value (Chown et al., 2001; Jones et al., 2003). They house a range of

endemic species, act as refugia for threatened flora and fauna, and attract attention from reintroduction biologists (Serena, 1995; Burbidge, 1999; Abbott, 2000). An understanding of the magnitude and significance of biopedturbation in these systems will aid in their management.

Procellariids, the 'tube-nosed' seabirds, such as *Puffinus* spp., nest colonially in burrows on islands (Serventy et al., 1971; Marchant and Higgins, 1990). Their biopedturbatory impacts may be physical, via digging and trampling, or chemical through nutrient input (predominantly through guano deposition, Furness, 1991; Butler, 1995; Sanchez-Pinero and Polis, 2000). Ecological studies of burrowing seabirds and their habitat have largely focussed on chemical soil properties and nutrient-vegetation associations (Gillham, 1963; Anderson and Polis, 1999; Mulder and Keall, 2001). Physical properties have largely been dismissed or ignored (Charman and Murphy, 2000). On Rottnest Island, Western Australia, the burrows of Wedge-tailed Shearwaters, *Puffinus pacificus*, have been estimated to displace 210 t of soil ha⁻¹; a rate in excess of many mammalian biopedturbators (Bancroft et al., 2004b). Therefore, the Wedge-tailed Shearwater colonies on Rottnest Island provide an excellent model to investigate biopedturbation by burrowing seabirds in an island ecosystem.

We predicted that biopedturbation by Wedge-tailed Shearwaters should affect a suite of chemical and physical soil properties in a similar manner to that reported in mammalian studies. In experimental manipulations that excluded the input of guano, we expected that biopedturbation alone should not significantly change chemical properties of the soil but might alter physical properties. Here we present our examination of the temporal and spatial patterns in physical (temperature, bulk density, water content, strength, water repellency, hydraulic conductivity) and chemical (nutrient composition, organic matter content, pH, conductivity) soil properties of the shearwater colonies and adjacent, non-colonised heath on Rottnest Island.

Materials and methods

Study site description and shearwater breeding phenology

The study was conducted between March 2002 and May 2003 on Rottnest Island (32°00'S, 115°31'E), a 1900 ha limestone island situated 18 km off the coast of Fremantle, Western Australia (Playford,

Table 1. Soil properties, and the sites and locations at which they were measured during the study

	Shearwater digging activity	Rate of guano deposition	Guano nutrient content	Soil surface temperature	Soil bulk density and water content	Soil strength	Water repellency	Soil hydraulic conductivity	Chemical properties
<i>Site</i>									
Radar reef	X	X	X	X	X	X	X	X	X
Cape Vlamingh			X			X			
<i>Location</i>									
Spoil	X				X		X	X	X
Colony		X		X	X	X	X	X	X
Edge						X			
Heath				X	X	X	X	X	X
Simulated burrow					X		X	X	X

1983). Table 1 shows the sampling sites and locations for each of the components of this study. With the exception of soil strength and guano nutrient content, all properties, samples and measurements were taken from the Wedge-tailed Shearwater colony at Radar Reef (see Bancroft et al., 2004a). Soil strength recordings and guano samples were also taken at Cape Vlamingh (see Bancroft et al., 2004a). Colony vegetation was dominated by succulent Iceplant, *Mesembryanthemum crystallinum*, with the prostrate shrubs: Seaberry Saltbush, *Rhagodia baccata*; Bower Spinach, *Tetragonia implexicoma*; and *Threlkeldia diffusa*. Adjacent heath vegetation was dominated by the shrubs: Prickle Lily, *Acanthocarpus preissii*; Coastal Daisy, *Olearia axillaris*; Coast Beard Heath, *Leucopogon parviflorus*; and *Westringia dampieri*. The geology of both colony and heath areas was the same, with a mixture of calcareous and siliceous sands overlaying a cemented limestone formation known as Tamala Limestone (Playford, 1983).

Within the sites, measurements or samples were taken from randomly chosen points from one or more of the following locations:

Spoil: Spoil piles at the entrance of shearwater burrow within the shearwater colony.

Colony: All other, non-spoil pile areas within the shearwater colony, where burrow density was greater than $0.15 \text{ burrows m}^{-2}$ (see Bancroft et al., 2004a).

Edge: The transition area between colony and adjacent heath, where burrow density was >0 and $\leq 0.15 \text{ burrows m}^{-2}$ (see Bancroft et al., 2004a).

Heath: Heath adjacent to the shearwater colony where burrow density was zero.

Simulated burrow: Spoil piles at the entrance of man-made, simulated burrows located within heath adjacent to the shearwater colony.

Table 2 presents the month(s) when samples were taken, and the number of samples or days (where appropriate) from which measurements were taken.

Wedge-tailed Shearwaters demonstrate a strong breeding phenology and, on Rottnest Island, the breeding season runs from approximately the 18 August to the 15 May (271 days, Garkaklis et al., 1998b). Birds migrate away from the island for the remainder of the year (94 days, Marchant and Higgins, 1990). Adult shearwaters arrive in mid-August to begin burrow excavation/clearing and courting (Garkaklis et al., 1998b). A 2-week pre-laying exodus occurs in early November, with eggs laid and incubated from late November (Garkaklis et al., 1998b). Chicks hatch from mid-January, are reared from January to late April, and fledge by mid-May (Johnstone and Storr, 1998). We used the following terms and notation to categorise the reproductive cycle into five phases: absent (A: birds not present), clearing (C: burrow clearing, courting, and pre-laying exodus), laying (L: egg laying), rearing (R: chick hatching and rearing), and fledging (F: chick fledging).

Shearwater digging activity

Thirty-five burrows were randomly chosen prior to the 2002/2003 breeding season and permanently marked. The digging activity of the shearwaters was assessed by placing an $80 \times 80 \text{ mm}^2$ ceramic tile on the spoil pile of the burrows in a position that would intercept soil ejected from the burrow. Tiles were visually inspected each morning. Burrows were scored as 'disturbed' if the tile was covered with sand, and 'undisturbed' if the tile remained exposed. Ten tiles were placed outside of the colony, to control for non-bird disturbances. All tiles were cleaned and repositioned prior to the

Table 2. Number of samples or days (for each of the locations) from which measurements were taken for each soil property studied

Property	Year and Month														
	2002						2003								
	March	April	May	June	July	August	September	October	November	December	January	February	March	April	May
Shearwater digging activity				4	8	1	3	7		9		8	4	4	8
Rate of guano deposition								1				6			
Guano nutrient content															
Soil surface temperature	10	8						9				15	5		
Soil bulk density and water content	5	5		5		b		5		5 ^a		5 ^a _b		5	
Soil strength															
Water repellency	5			5				5		5 ^a		5 ^a			
Soil hydraulic conductivity	5			5				5		5 ^a		5 ^a			
Chemical properties										5 ^c		5 ^c			

^aThree samples taken from Simulated Burrows.^bVariable sampling between locations—see text for details.^cTwo samples taken from Simulated Burrows.

arrival of adult shearwaters each evening. Digging activity was monitored on 43 nights during the breeding season (16% of the season) and 13 nights during the non-breeding season (14%). Data were analysed by a single-factor (reproductive phase), repeated-measures (burrows) ANOVA of the mean proportion of nights that a burrow was disturbed.

Guano nutrient content

Guano was collected from 16 individual shearwaters by holding them in metabolic cages overnight. Guano was pooled, oven-dried at 35 °C and sent to the Chemistry Centre of Western Australia for analysis. Nitrogen was determined by a combustion method (AOAC, 1990), using a LECO FP-428 Nitrogen Determinator. Phosphorus, potassium, calcium, magnesium, sulphur, boron, copper, iron, manganese, and zinc were determined by inductively coupled plasma atomic emission spectroscopy (ICP-AES) after digestion with a mixture of nitric and perchloric acids (McQuaker et al., 1979).

Rate of guano deposition

Guano traps (610 × 915 mm², brown, masonite boards) were randomly placed on the surface of both the shearwater colony and the adjacent heath. Boards were collected after 13 days and photographed. Guano deposited on boards was obviously white and the percentage of the surface area of each trap that the guano covered was determined using the ImagePro software package. In addition, 10 droppings were collected on aluminium foil placed beneath birds in holding cages and the relationship between surface area and dropping mass was determined. This was used to convert colony surface area measurements to mass.

Soil surface temperature

Temperature measurements were made using HOBO[®]-TEMP Temperature loggers (Onset Computer Corporation, Pocasset, MA, 02559) that were randomly placed on the soil surface. Data were downloaded using LogBook for Windows version 2.03. Mean temperatures were analysed with a two-factor (time of day, location), repeated-measures (burrows) ANOVA.

Soil bulk density and water content

Bulk density and water content were calculated using the methods in Millar et al. (1965). Soil cores

were collected using a 294 cm³, metal, soil ring, and returned to the laboratory for analysis. Samples were weighed, oven-dried at 105 °C for at least 48 h, and reweighed. Water loss was calculated and expressed as a percentage of the core volume. Bulk density was expressed as mass of dried soil per unit volume (g cm⁻³). Soil porosity was calculated following the equation provided by [Charman and Murphy \(1992\)](#), using a specific gravity of 2.65 g cm⁻³ as reported for quartz by [Baize \(1993\)](#). Data were analysed with a two-factor (location, time) MANOVA of the mean bulk density and water content (variables), and discriminant function analysis (DFA).

Soil strength

Soil strength, as measured by penetration resistance ([Geeves et al., 2000](#)), was investigated at two depth strata from three locations, within each of two sites ([Table 1](#)). Penetration resistance was measured using a RIMIK CP 20 Cone Penetrometer. The penetrometer probe was manually pushed into the soil, to a depth of 600 mm, with force readings recorded at 20 mm intervals. Each sample was the average of three penetrations. At Cape Vlamingh, 32 random samplings were taken from colony and heath, and 16 from edge locations. At Radar Reef, 40 samplings were taken from colony and heath, and 20 from edge locations. Sample numbers varied because of spatial limitations. Half of these recordings were made in August 2002, and half in February 2003. Penetration resistance was averaged for each of two strata (variables): 0–100 and 500–600 mm, and analysed with a two-factor (site, location) MANOVA.

Water repellency

Each sample was an approximately 200 g sub-sample of five thoroughly combined 100 g soil scrapes taken from a 10 × 10 cm² area of the soil surface (to 2 cm depth). Samples were returned to the laboratory and dried at 30 °C for at least 48 h. Water repellency was determined using the molarity of ethanol droplet (MED) method ([King, 1981](#)); repellency was expressed as the molarity of ethanol solution required to facilitate penetration of the soil by a droplet of solution. Increasing concentrations of ethanol droplets (0.2 M increments) were applied to the soil surface until penetration occurred within 10 s. Mean MED scores were analysed with a two-factor (location, time) ANOVA.

Soil hydraulic conductivity

Hydraulic conductivity, an index of soil permeability, was derived from measurements taken with a disc permeameter ([White et al., 1992](#)) following the field protocol of [Thony et al. \(1991\)](#) and the calculations of [Smettem and Bristow \(1999\)](#) and [Minasny and McBratney \(2000\)](#). On each occasion the leaf litter was gently cleared from the soil surface and the permeameter was placed on a levelled sand cap (1 cm depth). The water suction potential of the permeameter was set to 20 mm and the cumulative water infiltration was recorded manually at 10 s to 1 min intervals, where appropriate, until the permeameter's reservoir tower was empty. Mean hydraulic conductivities were analysed with a two-factor (location, time) ANOVA.

Soil nutrients, organic matter, pH, and conductivity

Approximately 100 g soil samples were taken from a 10 × 10 cm² area of the soil surface (to 2 cm depth), thoroughly combined, and a sub-sample of approximately 300 g was sent to CSBP FutureFarm Laboratories for analyses. Ammonium and nitrate analyses followed the methodology of [Searle \(1984\)](#), phosphorous and potassium followed [Colwell \(1965\)](#) and [Rayment and Higginson \(1992\)](#), sulphur followed [Blair et al. \(1991\)](#), organic carbon followed [Walkley and Black \(1934\)](#), and conductivity and pH followed [Rayment and Higginson \(1992\)](#). Iron was determined using a flame atomic absorption spectrophotometer after tumbling soil with Tamm's reagent. The mean chemical properties (variables) were analysed with a two-factor (location, time) MANOVA.

Simulated burrows

Forty simulated burrows were constructed in an area of non-colonised heath, adjacent to the colony at Radar Reef. Burrows were dug manually, using a 150 mm diameter auger and a hand trowel. Careful attempts were made to match the aspect, incline and dimensions of natural Wedge-tailed Shearwater burrows (see [Bancroft et al., 2004b](#)). Burrows for sampling (of bulk density, water content, repellency, hydraulic conductivity, and chemical properties) were randomly chosen and only sampled once. Methods for sampling were identical to the other locations. Data from simulated burrow were not collected at all time points, so were analysed separately using the methods describe above.

Descriptive statistics

Mean values are reported \pm standard deviation.

Results

Shearwater digging activity

Soil excavation was recorded from 94.3% of burrows on at least one night of the breeding season. The mean proportion of nights during breeding season on which soil was excavated from a burrow was 0.31 ± 0.15 (range 0.00–0.58). We found no difference in the excavation rate between individual burrows (RM-ANOVA, $F_{34,104} = 0.91$, $P = 0.613$), but the reproductive phase had a significant influence on the mean proportion of burrows excavated per night (Fig. 1, RM-ANOVA, $F_{4,31} = 38.07$, $P < 0.001$). Fig. 1 shows that the mean proportion of burrows excavated per night was greater in the burrow clearing and laying phases, with a decrease (in excavation rate) as the breeding season progressed through the rearing and fledging phases.

Guano nutrient content

A guano sample was analysed for 12 elemental compounds and the results are presented in Table 3. The main constituents of the guano were nitrogen (approximately 22%), potassium (2%),

sulphur (2%), phosphorus (1.5%), sodium (1.5%), and calcium (1.5%).

Rate of guano deposition

Wedge-tailed Shearwaters deposited guano on 0.08% of the colony's surface area each night ($8.0 \text{ cm}^2 \text{ m}^{-2} \text{ night}^{-1}$). The dry mass of deposited guano was $10.8 \pm 1.1 \text{ mg cm}^{-2}$ and the rate of guano deposition (dry mass) on the colony was $234.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The rates of elemental deposition are given in Table 3. No Wedge-tailed Shearwater guano deposition was recorded from the heath.

Soil surface temperature

Mean diurnal soil surface temperatures were 31.7 ± 6.2 (range 18.1–43.4) and 29.7 ± 6.6 (range 17.6–47.3) for the colony and heath, respectively. Mean nocturnal temperatures were 18.3 ± 3.2 (range 10.8–23.6) for colony and 18.5 ± 3.1 (range 11.6–24.1) for heath. Overall, there was a significant effect of location on mean temperature (RM-ANOVA, $F_{1,46} = 7.91$, $P = 0.007$), diurnal and nocturnal temperature differed significantly (RM-ANOVA, $F_{1,46} = 234.52$, $P < 0.001$), and there was a significant interaction between location and time of day (RM-ANOVA, $F_{1,46} = 9.78$, $P = 0.003$). Investigation of the interaction revealed that, while the colony was warmer than the heath during the day

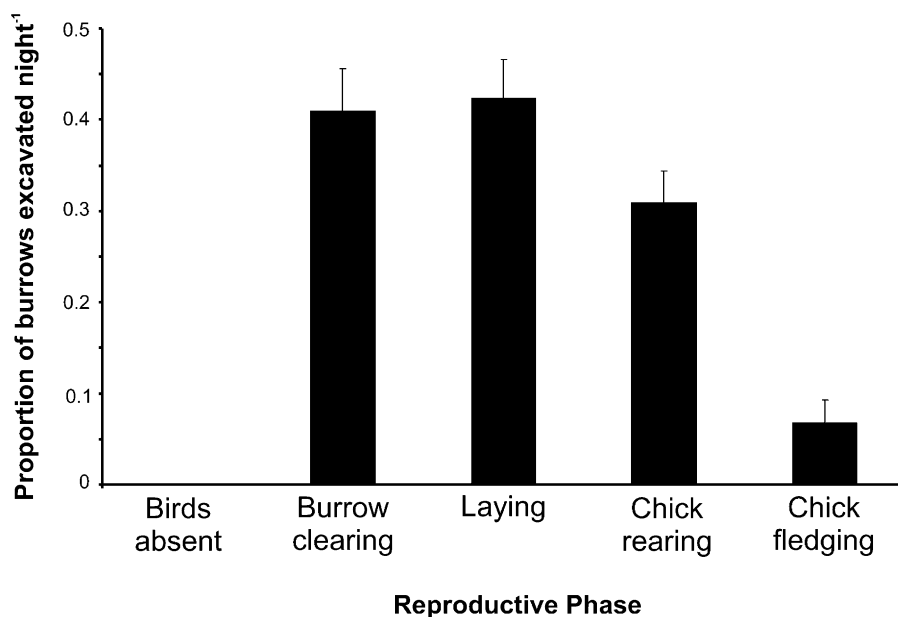


Figure 1. Mean (\pm SE) proportion of burrows at Radar Reef that were excavated per night during each phase of the Wedge-tailed Shearwater breeding cycle.

Table 3. Elemental content and deposition rate of Wedge-tailed Shearwater guano

Element	Content in guano (g kg ⁻¹)	Deposition rate (kg ha ⁻¹ yr ⁻¹)
Nitrogen	217.0	50.863
Potassium	24.2	5.672
Sulphur	23.4	5.485
Phosphorous	15.4	3.610
Sodium	14.8	3.469
Calcium	14.7	3.446
Magnesium	5.4	1.266
Zinc	1.2	0.281
Iron	1.0	0.234
Boron	0.033	0.008
Copper	0.02	0.005
Manganese	0.014	0.003

and cooler than the heath at night, the differences were not significant (SNK, $P > 0.2$).

Soil bulk density and water content

Both location (MANOVA, $F_{4,166} = 34.10$, $P < 0.001$) and time of year (MANOVA, $F_{12,166} = 20.216$, $P < 0.001$) had a significant impact on mean soil bulk density and mean soil water content (Fig. 2), and there was no significant interaction between the two (MANOVA, $F_{24,166} = 1.15$, $P = 0.295$). The mean soil bulk density of the spoil piles (1.30 ± 0.11 g cm⁻³) was significantly greater (SNK, $P < 0.001$) than the colony (1.19 ± 0.11 g cm⁻³) which was significantly greater (SNK, $P < 0.001$) than the surrounding heath (1.01 ± 0.07 g cm⁻³). These values equate to mean soil porosity values of 51%, 55%, and 62% for spoil, colony, and heath, respectively. Soil bulk density was significantly greater in December and February than in June and October (SNK, $P < 0.049$). Heath soil (8.41 ± 7.26 vol%) was significantly wetter (SNK, $P < 0.029$) than the colony (6.81 ± 5.79 vol%) and spoil piles (6.04 ± 5.40 vol%). Soil water content was similar in December, February, and March (SNK, $P > 0.814$), and in April and May (SNK, $P > 0.871$), but all other months differed significantly from each other (SNK, $P < 0.001$).

DFA revealed that bulk density was the main contributor to between location differences (DFA, function 1 explained 99.9% of variance, standardised discriminant function coefficients were 1.023 for bulk density, 0.126 for water content), while water content was mostly responsible for temporal variation (DFA, function 1 explained 98.9% of variance, standardised discriminant function coef-

ficients were 1.107 for water content, 0.104 for bulk density).

We found a significant difference overall (MANOVA, $F_{6,54} = 7.66$, $P < 0.001$), and in bulk density (ANOVA, $F_{3,28} = 19.46$, $P < 0.001$) but not water content (ANOVA, $F_{3,28} = 1.03$, $P = 0.393$) when we compared data from simulated burrows to the three other locations for December and February. The bulk density of the simulated burrows was significantly less than true spoil piles (SNK, $P = 0.005$), greater than heath (SNK, $P = 0.004$) and no different to colony soil (SNK, $P = 0.551$).

Soil strength

The penetration resistance (Fig. 3) of the Cape Vlamingh and Radar Reef sites was not significantly different (MANOVA, $F_{2,173} = 1.38$, $P = 0.253$), but it did differ between the sampling locations (colony, edge, and heath, MANOVA, $F_{4,346} = 44.78$, $P < 0.001$) and the interaction between site and location was not significant (MANOVA, $F_{4,346} = 1.62$, $P = 0.169$). For both the 0–100 and 500–600 mm soil depth strata, there was less resistance in the colony (326.5 ± 122.4 and 1116.8 ± 465.0 kPa, respectively) than the edge (446.8 ± 116.1 and 2350.8 ± 597.0 kPa) or heath (443.5 ± 115.2 and 2507.9 ± 855.3 kPa; SNK, $P < 0.001$). There was no difference in resistance between edge and heath soil at either of the depth strata (SNK, $P > 0.249$).

Water repellency

The mean MED score (Fig. 4) differed significantly between locations (ANOVA, $F_{2,60} = 71.04$, $P < 0.001$) and months (ANOVA, $F_{4,60} = 3.59$, $P = 0.011$), and there was no significant interaction (ANOVA, $F_{8,60} = 3.59$, $P = 0.384$). Heath soil (3.15 ± 0.60 MED) was more water repellent (SNK, $P < 0.001$) than colony soil (2.26 ± 1.04 MED) which was more repellent (SNK, $P < 0.001$) than spoil pile soil (0.55 ± 0.83 MED). Soils were significantly less wettable in July than in March (SNK, $P = 0.004$), but there was no difference between the water repellency of soils from any other months (SNK, $P > 0.066$).

There was a significant difference in water repellency when simulated burrows were compared to the three other locations for December and February (ANOVA, $F_{3,26} = 25.06$, $P < 0.001$). Water repellency of the simulated burrows was no different to the true spoil piles (SNK, $P = 0.999$), and was less than both colony (SNK, $P = 0.003$) and heath (SNK, $P < 0.001$) soil.

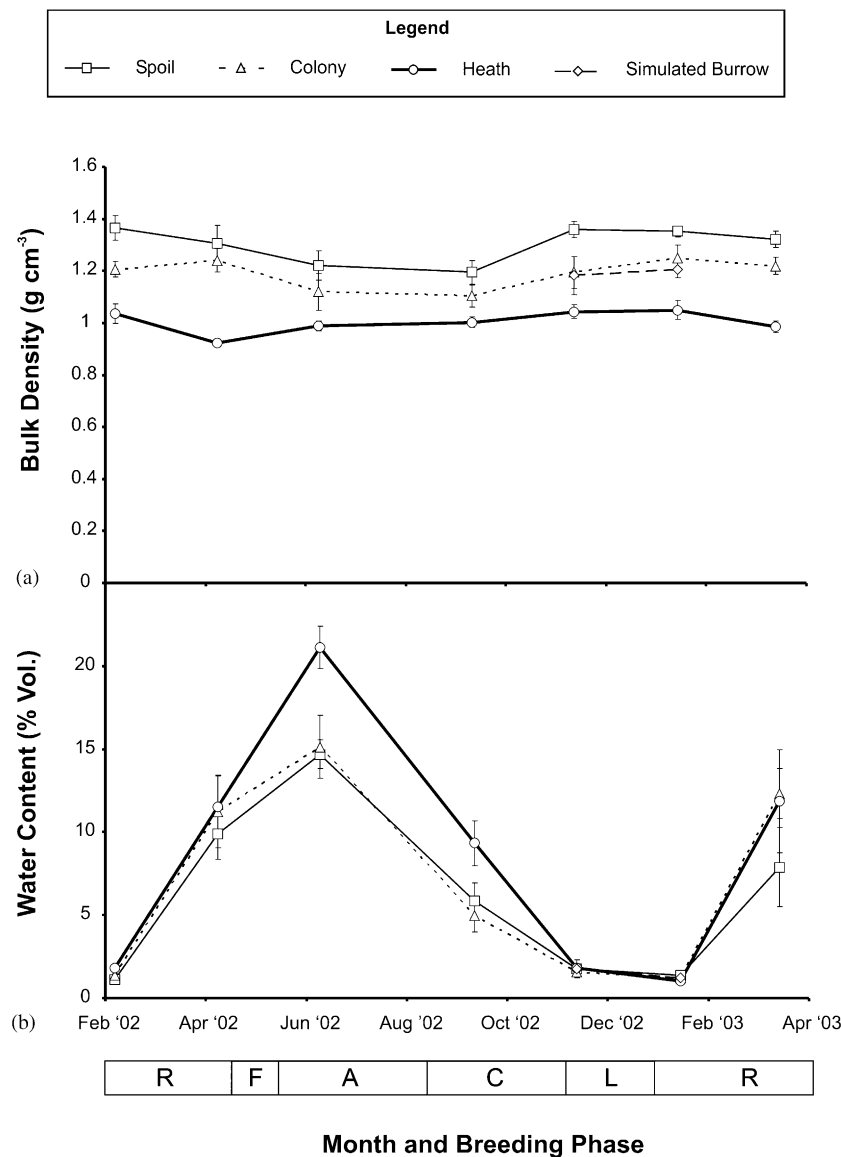


Figure 2. Mean (\pm SE) soil bulk density (a) and water content (b) at each of four locations: spoil, colony, heath, and simulated burrows. See Materials and methods for breeding phase abbreviations (A, C, L, R, F).

Soil hydraulic conductivity

The hydraulic conductivity of surface soil (Fig. 5) was significantly different between locations (ANOVA, $F_{2,60} = 33.75$, $P < 0.001$) and between months (ANOVA, $F_{4,60} = 8.05$, $P < 0.001$); however, the interaction term was also significant (ANOVA, $F_{4,60} = 4.64$, $P < 0.001$). The latter probably reflects the disproportionate decrease in conductivity across locations, between July and October (Fig. 5). Soil from spoil piles ($398.91 \pm 252.04 \text{ mm h}^{-1}$) was significantly more conductive than the colony ($192.45 \pm 124.10 \text{ mm h}^{-1}$), which was more conductive than the heath ($108.97 \pm 99.87 \text{ mm h}^{-1}$; SNK,

$P < 0.025$ in each case). Only the hydraulic conductivity of the spoil pile soil varied significantly between months, with October significantly less conductive (SNK, $P < 0.05$), and December significantly more conductive (SNK, $P < 0.05$) than all other months (Fig. 5). Spoil pile soil was significantly more conductive (SNK, $P < 0.05$) than colony and heath soil in December and March, and more conductive (SNK, $P < 0.05$) than heath soil in February (Fig. 5).

Hydraulic conductivity differed significantly with location when simulated burrows were compared to the three other locations for December and February (ANOVA, $F_{3,28} = 15.92$, $P < 0.001$).

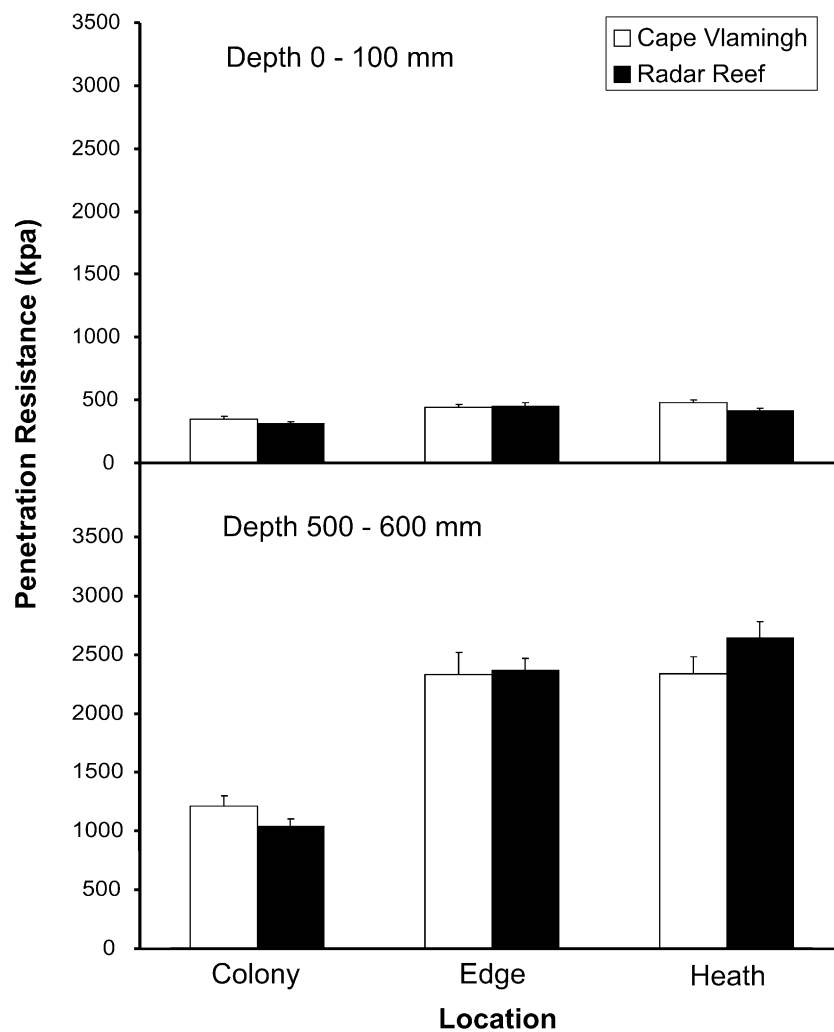


Figure 3. Mean (\pm SE) soil strength at two depth strata (0–100 and 500–600 mm) from the colony, edge, and heath locations at Cape Vlamingh and Radar Reef.

Simulated burrows had a similar hydraulic conductivity to the true spoil piles (SNK, $P = 0.237$), which was greater than both colony (SNK, $P = 0.009$) and heath (SNK, $P = 0.001$) soils.

Soil nutrients, organic matter, pH, and conductivity

Soil chemical properties (nutrient, pH, and conductivity levels, Fig. 6) differed significantly over time (MANOVA, $F_{45,289} = 9.48$, $P < 0.001$) and between sampling locations (MANOVA, $F_{18,128} = 47.20$, $P < 0.001$); however, the pattern of variation was not consistent across all chemical properties, locations, and dates (significant interaction term; MANOVA, $F_{90,444} = 2.56$, $P < 0.001$). All chemical properties demonstrated a significant difference between locations (for all cases, ANOVA,

$F_{2,72} > 16.52$, $P < 0.001$), and all but phosphorous (ANOVA, $F_{5,72} = 1.73$, $P = 0.139$) and iron (ANOVA, $F_{5,72} = 2.11$, $P = 0.074$) were significantly different across time (for all other cases, ANOVA, $F_{5,72} > 4.85$, $P < 0.001$). The direction and significance of differences in chemical properties between locations are summarised in Table 4. Nitrate and conductivity levels were higher in the spoil than the colony, which had higher levels than the heath. There was no difference in the sulphur or ammonium content of the colony and heath, but both these locations had lower levels than the spoil. Heath soil had significantly less potassium, and significantly more iron, than either spoil or colony soils. Phosphorous and pH were lowest in the heath, with colony having higher levels than spoil. The organic carbon content of the spoil was lower than the colony, which was lower than the heath.

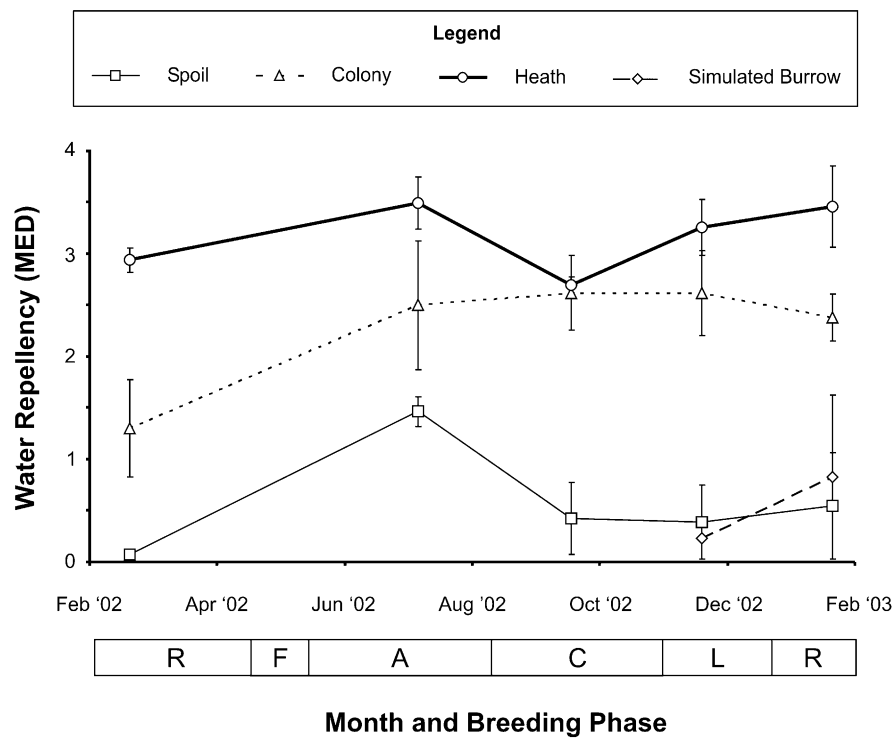


Figure 4. Mean (\pm SE) water repellency of spoil, colony, heath, and simulated burrow soil. See Materials and methods for breeding phase abbreviations (A, C, L, R, F).

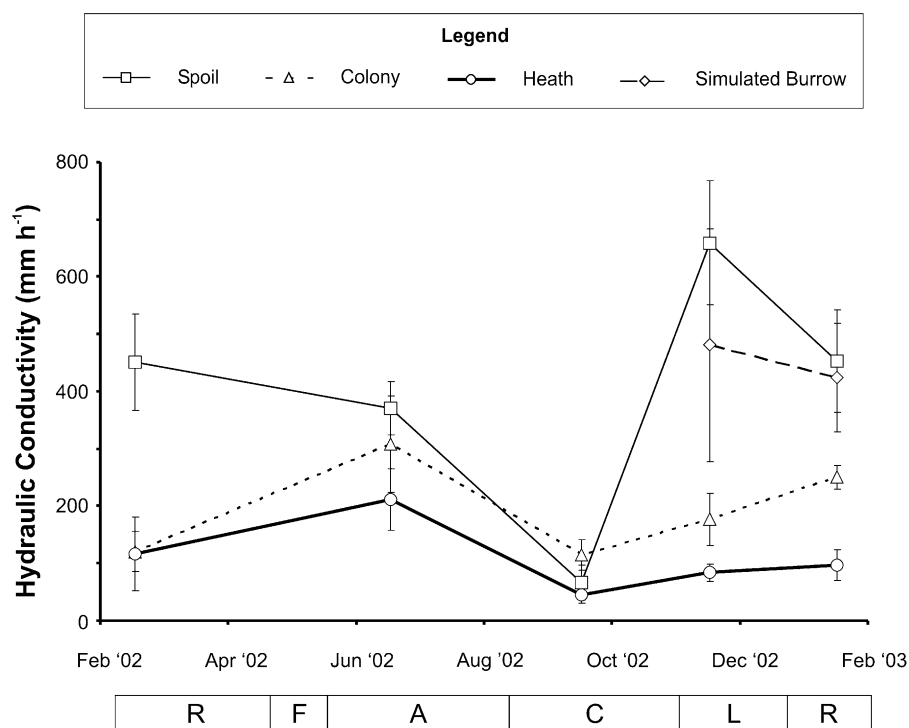


Figure 5. Mean (\pm SE) hydraulic conductivity of spoil, colony, heath, and simulated burrow soil. See Materials and methods for breeding phase abbreviations (A, C, L, R, F).

All chemical factors at simulated burrows were compared to the three other locations for December and February and there was an overall influence of location (MANOVA, $F_{27,53} = 13.85$, $P < 0.001$) and date (MANOVA, $F_{9,18} = 4.61$, $P = 0.003$), but no interaction (MANOVA, $F_{27,53} = 0.94$, $P = 0.559$). All chemical properties differed significantly between locations (for all cases, ANOVA, $F_{3,26} > 5.66$, $P < 0.004$), but only potassium and ammonium differed between the months (for both cases, ANOVA, $F_{1,26} > 9.53$, $P < 0.005$). There was no difference in the levels of phosphorous, nitrate, ammonium, sulphur, and conductivity between the simulated burrows and heath soil (SNK, $P > 0.055$). Potassium, iron, and organic carbon were reduced in the simulated burrow soil, when compared to the heath (SNK, $P < 0.011$), while pH was significantly increased (SNK, $P = 0.011$).

Discussion

Overall impact of shearwater biopedturbation

The Wedge-tailed Shearwater of Rottnest Island is an excellent example of a vertebrate biopedturbator that is modifying an island ecosystem. Here we have shown that soil is excavated from the burrows throughout the breeding season, with any given burrow excavated about once every three nights; presumably in order to maintain the integrity of the burrows. Consequently, there is a considerable physical disturbance of the soil by the birds. In addition, the shearwaters deposit nitrogen-rich guano on 21.7% of the colony in a breeding season. The deposition contributes nearly 51 kg of nitrogen $\text{ha}^{-1} \text{yr}^{-1}$. By comparison, the majority of the south western Australian agricultural area is fertilised with nitrogen at a rate of 8–20 kg $\text{ha}^{-1} \text{yr}^{-1}$ (Rau-pach et al., 2001). Biopedturbation by shearwaters on Rottnest Island stands out in a system that is devoid of vertebrate biopedturbators of a similar magnitude.

We correctly predicted that, like their mammalian counterparts, biopedturbation by shearwaters should modulate soil properties. For all physical and chemical soil properties measured in our study, there was a significant difference between at least one of the locations where the birds had disturbed the soil (colony, spoil, edge) and the adjacent, undisturbed area (heath). In comparison to the surface soil of the heath, the biopedturbated soil had greater bulk density, increased wetting capacity and water infiltration, reduced penetration resistance, was drier, and experienced a greater

range in temperature. This soil also had increased levels of nitrate, phosphorous, ammonium, sulphur, and potassium, decreased levels of iron and organic carbon, was more alkaline and had greater conductivity. All the soil properties investigated in this study have been previously investigated by mammalian biopedturbation studies (Table 5). The variation in results between studies is striking and probably reflects variation in soil type, climate, and degree of disturbance. No factor in our study remained unchanged. This may indicate that avian biopedturbators in a Mediterranean, island ecosystem have greater influence on ecosystem function than small mammals (Titus et al., 2002), kangaroos (Eldridge and Rath, 2002) or woylies (Garkaklis et al., 2003) in arid and semi-arid continental ecosystems.

Mulder and Keall (2001) found that soil properties were correlated with the degree of disturbance (burrow density). While we did not look specifically for graded changes in soil properties within the colony, locations within the colony with varying levels of disturbance suggested such a pattern also occurs on Rottnest Island. For all physical properties, and all but two chemical properties (iron and potassium), there was a significant difference between areas with different magnitudes of shearwater disturbance.

The spatial heterogeneity imposed by seabird digging within colonies does not appear to override seasonal effects. Natural, temporal fluctuations in physical or chemical properties that occurred in undisturbed heath were also evident in disturbed areas. In some cases, such as water content and nitrate levels (Figs. 2 and 6), the magnitude, but not the direction, of the fluctuation was altered by biopedturbation. Soil properties in both biopedturbated and undisturbed areas also behaved similarly during the transition period between the presence and absence of shearwaters on the island. So, while biopedturbation by shearwaters drives strong spatial changes in soil properties, temporal variability appears to be driven by overriding climatic cycles, particularly rainfall events (Hasset and Banwart, 1992; Chapin et al., 2002).

Impact of physical biopedturbation

While it is often difficult to tease apart the effects of chemical and physical inputs, we attempted to examine the contribution of digging, alone, by comparing simulated burrows (with no input of guano) to the heath. A single episode of simulated burrow creation, timed to coincide with the natural clearing period of the shearwaters, was sufficient

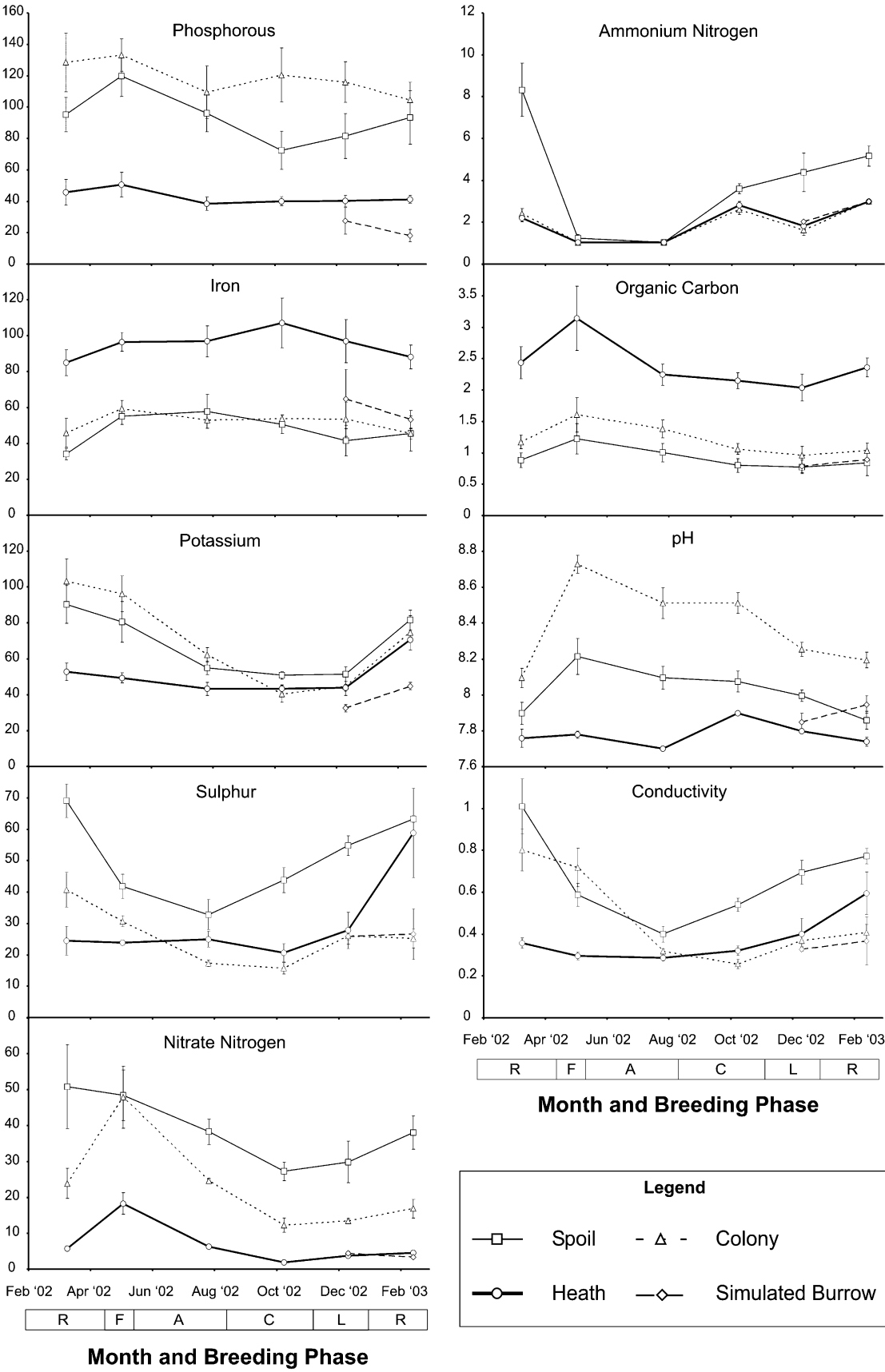


Table 4. Direction and significance of differences in the chemical properties of spoil, colony, and heath soils

Difference	Chemical property
Spoil > colony > heath	Nitrate nitrogen (<0.001, <0.001, <0.001) Conductivity (<0.001, <0.001, 0.004)
Spoil > (colony = heath)	Sulphur (<0.001, <0.001, 0.137) Ammonium nitrogen (<0.001, <0.001, 0.891)
(Spoil = colony) > heath	Potassium (0.599, <0.001, <0.001)
(Spoil = colony) < heath	Iron (0.324, <0.001, <0.001)
(Spoil < colony) > heath	Phosphorous (<0.001, <0.001, 0.004) pH (<0.0001, <0.001, <0.001)
Spoil < colony < heath	Organic carbon (0.019, <0.001, <0.001)

Note: Probabilities given are SNK post hoc results for spoil vs. colony, spoil vs. heath, and colony vs. heath, respectively.

to alter three out of four physical properties tested. Simulated burrow soil, like that of the true biopedturbated areas, had increased soil bulk density, increased wetting capacity and increased water infiltration rate, relative to undisturbed heath soil. While no difference was observed in the soil water content, samples were taken only in summer, the period of lowest water content and least variation across all locations (Fig. 2), so this result should be interpreted cautiously. Digging alone produced changes in four out of the nine chemical properties. Alkalinity was increased, and iron, potassium, and organic carbon levels were decreased. Zhang et al. (2003) found that the potassium content of soil decreased rapidly with increased depth below the surface. The results obtained in our study may be explained by naturally nutrient poor burrow ejecta (as noted by Zhang et al., 2003) or, alternatively, a more complex mineralisation process may be initiated by biopedturbation and the exposure of sub-surface soil to the atmosphere. As expected, for the four major elemental constituents of guano (Table 3) there was either a decrease or no difference in the levels observed at the simulated burrows. We have shown that physical soil properties are most tightly bound

to physical biopedturbation. For these properties the more frequently disturbed locations always had readings that fell at the extreme of the values for that property, confirming that increased biopedturbation magnifies changes in physical soil properties (Mulder and Keall, 2001).

Sanchez-Pinero and Polis (2000) categorised four ways by which seabirds may affect terrestrial biota: guano, carrion, living tissue, and flow through effects of primary productivity, yet did not make mention of physical input (e.g. digging, trampling). The physical modification of habitat by seabirds (ecosystem engineering, Jones et al., 1994) has now been shown to modulate the availability of resources to other species. These effects can be direct (e.g. use of Fairy-prion, *Pachyptilla turtor*, burrows as shelter by Tuatara, *Sphenodon punctatus*, Newman, 1987) or indirect, by modulating both physical and chemical soil properties, as our simulated burrow findings have shown. It is not only the allochthonous chemical input (Markwell and Daugherty, 2002) that is important in these burrowing seabird colony systems; the birds' physical input is also significant. The alteration of the physical properties of soil by seabird biopedturbation, unstudied by other authors (Anderson and Polis, 1999; Sanchez-Pinero and Polis, 2000), is likely to interact directly with soil chemistry. Gillham (1960) suggested that islands in wetter latitudes had fewer plants 'burnt' by nutrients because of the rapid leaching of nutrients, and argued that chemical input was more important than physical biopedturbation. Clearly, however, this is an interaction between physical and chemical soil processes. On Rottneest Island, we have shown that physical biopedturbation can increase soil water content, repellency, and hydraulic conductivity; factors that can accelerate the leaching of nutrients. So, while it is the chemical inputs that directly influence plant health and composition (Gillham, 1960), physical properties, regardless of whether they are driven by climate or biopedturbation, may modulate the chemical, and should not be dismissed.

Modification of physical soil properties by shearwaters also has the potential to affect the vegetation community directly. The main mechanism is via disruption of the soil water that is responsible for the delivery of nutrients to plant tissues (Crawley, 1986). Soil temperature, bulk density, water content, strength, repellency, and hydraulic conduc-

Figure 6. Mean (\pm SE) chemical properties of spoil, colony, heath, and simulated burrow soil. All units are mg kg^{-1} , except for organic carbon (%), pH (pH units), and conductivity (dS m^{-1}). See Materials and methods for breeding phase abbreviations (A, C, L, R, F).

Table 5. Comparison of the influence of some mammalian biopedturbators and Wedge-tailed Shearwaters (this study) on soil properties

Soil property	Increased	No change	Decreased
Soil surface temperature	This study Plateau zokor ^a		
Soil bulk density	This study	Kangaroos ^b	Banner-tail Kangaroo Rat, Wyoming ground squirrel, and Townsend's Ground Squirrel ^d
Soil strength	Kangaroos ^b	European rabbit ^c	This study Plateau Zokor ^a
Water content			This study Gerbils ^d Plateau zokor ^a
Water repellency	Woylie ^e		This study Woylie ^f
Infiltration	This study Rodents, Cansu Mole Rat, and gerbils ^d	Small mammals ^g Kangaroos ^b	
Phosphorous	This study Prairie dog and geomyids ^d Small mammals ^g Plateau zokor ^a	Woylie ^h	
Iron	Cottontail rabbit, Southern Tuco-tuco, gerbils, Red Viscacha Rat, and Bathyergid mole rats ^d	Woylie ^h	This study
Potassium	This study Geomyids, Southern Tuco- tuco, gerbils, Red Viscacha Rat, and Bathyergid mole rats ^d	Woylie ^h Small mammals ^g	
Sulphur	Plateau zokor ^a This study Kangaroos ^b		Woylie ^h
Nitrate nitrogen	This study Small mammals ^g		Woylie ^h Prairie dog and mole rats ^d
Ammonium nitrogen	This study	Small mammals ^g	Woylie ^h
Total nitrogen	Mole rat, kangaroo rats, Cottontail Rabbit, Southern Tuco-tuco, gerbils, Red Viscacha Rat, and Bathyergid mole rats ^d Plateau Zokor ^a Kangaroos ^b		
Conductivity	This study Kangaroos ^b European Rabbit ^c		
pH	This study Prairie dog ^d	Woylie ^h Small mammals ^g Kangaroos ^b	European rabbit ^c
Organic carbon	Mole rat, kangaroo rats, and Cottontail Rabbit ^d Kangaroos ^b	Woylie ^h Small mammals ^g	This study Mole rats ^d Plateau zokor ^a

^aZhang et al. (2003).^bEldridge and Rath (2002).^cEldridge and Myers (2001).^dWhitford and Kay (1999).^eGarkaklis et al. (2000).^fGarkaklis et al. (1998a).^gTitus et al. (2002).^hGarkaklis et al. (2003).

tivity all directly affect the infiltration, percolation, permeability, and rate of flow of water into, and through, the soil (Charman and Murphy, 2000). In addition, soil temperature will affect the rate and direction of physical (e.g. evaporation, flow of water vapour, soil aeration), chemical and biological (e.g. seed germination, root growth, water and nutrient absorption, microbial activity) processes (Millar et al., 1965). Compaction of soil by shearwaters, as evidenced by higher soil bulk densities, destroys the larger, more fragile pores within soil (Hasset and Banwart, 1992). Air movement is dependent on these macropores (Baize, 1993), and will be reduced in shearwater disturbed areas. The reduced strength of colony soil may affect plant root morphology and plant stability, with roots more easily penetrating these areas (Millar et al., 1965). On islands such as Rottnest, where burrowing seabird colonisation has been a relatively recent phenomenon (Bancroft et al., 2004a), these physical factors, in association with increased nutrient deposition and a high level of soil turnover, will favour colonisation by coprophilic, exotic plant species (Rippey et al., 2002). In this situation, native species that are adapted to weakly disturbed, nutrient poor soil are unable to compete with exotic plants.

Concluding remarks

Due to their recent establishment on Rottnest Island, the Wedge-tailed Shearwaters may be classed as ecosystem-engineering, biological invaders (Crooks, 2002). Crooks (2002) highlights the impacts and importance of such biological invaders, and echoes calls from the ecosystem engineering literature (Jones et al., 1994, 1997; Gurney and Lawton, 1996) for researchers to begin "identifying and quantifying resources affected". We have begun that process for the Wedge-tailed Shearwater of Rottnest Island at the basal level; the soil environment. Our data are useful, in that we have shown that burrowing seabirds, as either biological invaders, ecosystem engineers or simply bioped-turbators, significantly alter the chemical and physical properties of soils, and we have quantified these changes. In the ecosystem view, these perturbations are likely to exert major bottom-up influences on the plant and animal communities of Rottnest Island. Clearly, these burrowing seabirds dominate parts of the terrestrial ecosystems they inhabit, and their capacity to alter the environment, particularly in regard to issues involving the conservation of island biodiversity, should not be ignored.

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