ECOLOGICAL STUDIES OF VEGETATION IN SHORT-TAILED SHEARWATER COLONIES IN TASMANIA

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(with two text-figures and three tables)

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Forestry Commission, 199 Macquarie Street, Hobart, Tasmania, Australia 7000 (MJB and KJW); University Tokyo Noko, Tokyo, Japan (NM).
Extensive modification of coastal vegetation at the Pineapples and Cape Deslacs rookeries is related to the burrowing, trampling and guano deposition of short-tailed shearwaters (*Puffinus tenuirostris*). Ordination and classification of the associated vegetation and measurement of soil nutrient levels demonstrate two distinct but interacting phases of vegetation succession. These are affected by coastal influence, edaphic factors and the presence or absence of nesting areas.
Key Words: vegetation, soil nutrients, shearwater, ecological studies, Tasmania.

INTRODUCTION

The short-tailed shearwater (*Puffinus tenuirostris*) is a major ecological, cultural and sometimes economic feature of the Tasmanian coastal landscape.

In a classic series of papers, Gillham (1958, 1960, 1961, 1965) elucidated the characteristics of the vegetation of Tasmanian short-tailed shearwater colonies in the Furneaux Group of islands in Bass Strait. Her papers also provide some indications of the soil conditions which prevail at rookery sites.

During the 1970s and 1980s staff from the State Wildlife agency (currently the Parks and Wildlife Service, Department of Environment and Land Management) have continued the long-term studies, begun in the late 1950s by D. Serventy and then carried on by V. Serventy, into the life cycle and dynamics of the short-tailed shearwater (e.g. Serventy 1958, 1967, 1968, Skira *et al.* 1986). These studies have been broadened to encompass statewide inventory and monitoring of the effects of commercial and non-commercial exploitation of the birds for human consumption (e.g. Naarding 1981, Skira 1990).

The succession of vegetation in coastal areas of Tasmania has been examined in detail at several sites around the state. Thus Bowden & Kirkpatrick (1974) have outlined the progression of vegetation from the shore to the saltmarsh hinterland at Rheban Spit in the southeast and Brown (1980) outlined a putative successional scheme for the western coastal vegetation at Mt Cameron West. More recently Chladil & Kirkpatrick (1989) undertook a quantitative study of the dune vegetation at Asbestos Range National Park in the north.

Whilst there has been considerable study of the birds and of their habitats, there has been little attempt to relate the dynamics of the birds *in situ* and the ecological succession of vegetation at the rookeries. The present paper attempts to provide a first examination of these interrelationships at two rookeries, Pineapples and Cape Deslacs, and includes relevant comment from elsewhere.

METHODS

Studies of Site Vegetation and Soil

The vegetation at Pineapples and Cape Deslacs (fig. 1) was sampled on several occasions during Dec/Jan 1987/88 and in 1989/90 using 2 × 2 m quadrats. Each species was scored for its abundance using a modified Braun-Blanquet score. Vascular plants only were scored.The species nomenclature used in this paper follows Buchanan *et al.* (1989). The species presence data from Pineapples were subjected to ordination and classification using detrended correspondence analysis (DCA) and TWINSPAN respectively (Hill 1979a, b). Only two axes were selected from the ordination, as the later axes are known to be non-linear combinations of axes one and two (P. Minchin, pers. comm.).

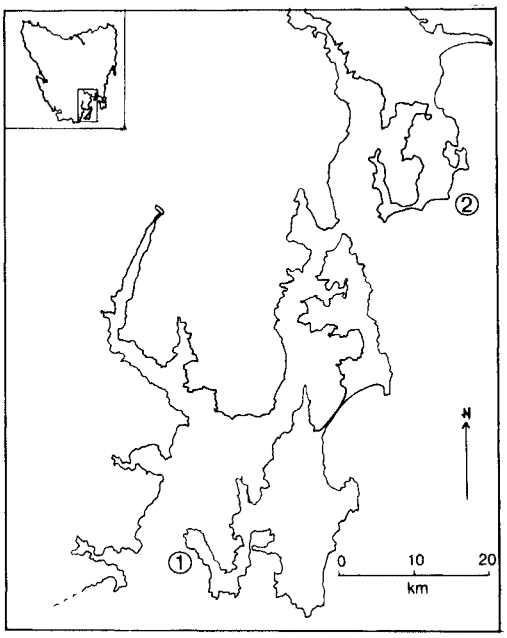

FIG. 1 — Locations of study sites: (1) Pineapples; (2) Cape Deslacs.

Total vegetation cover, rock cover and sand cover was classified, and an assessment was made of the number of burrows, the recency of occupancy and the amount of disturbance at each site.

Soils were collected at Pineapples (14 samples) and at Cape Deslacs (17 samples) to encompass the range of vegetated environments encountered at each site. Soil analyses were conducted for us by the Tasmanian Department of Primary Industry's analytical laboratories. Soil characteristics measured were pH (aqueous extract), conductivity (aqueous extract), P, K, N, Ca, Mg and Na (bicarbonate extract). Organic carbon content was requested but measurement facilities were not available.

In order to analyse numerically the relationships between soils and the vegetation, the data from Pineapples were subjected to factor analysis and subsequent varimax rotation. The DCA scores were incorporated into these analyses together with pH, conductivity and the logarithms of the concentrations of P, K, N, Ca, Mg, and Na in ppm.

Site Descriptions

The rookeries at Pineapples are underlain by aeolian sands which, in turn, overlie Jurassic dolerite. The rookeries are on an exposed westerly aspect and extend from a few metres inland of the unvegetated coastal rocks to about 300 m inland. The area was burnt in the bushfires of 1966/67, and parts of the area were burnt again in 1982.

The cliffs at Cape Deslacs are formed of Permian sediments (Parmeener supergroup) and rise to 54 m. These cliffs are also overlain by aeolian sands, which are of sufficient depth to support short-tailed shearwater colonies. The colonies here are found on all aspects, the bluff forming an indented headland which projects into the sea to the southeast and which also falls away from a high point towards the north. The rookeries occupy the cliff tops and extend about 150–200 m inland. This area was probably also burnt in 1967, but no clear evidence of the age of the vegetation was obtained.

RESULTS

The results of the analysis by Twinspan are shown in table 1. The descriptions of the communities at Cape Deslacs and at Pineapples which follow are based on this classification but have been modified to accord with field observations.

The Vegetation

The plant communities at both sites are of similar composition. Near the coast there is a halophytic community dominated by various combinations of *Disphyma australe, Tetragonia implexicoma, Carpobrotus rossii, Stipa stipoides, Leucopogon parviflorus, Poa poiformis, Poa labillardierii, Scirpus nodosus* and *Rhagodia baccata.* These communities have a range of structures depending on their physiographic situation. On deep soils on cliff ledges and declivities, the shrubs predominate and form open shrublands, whilst open grasslands of *Stipa stipoides/Poa poiformis* or succulent herbfields occur on the shallow soils of the exposed cliff tops and rock faces. Other cliff top shrub elements include *Helichrysum reticulatum* and *Olearia phlogopappa.*

Small saline soaks and wet patches are found on drainage lines in shallow soils of the cliffs and support non-succulent salt-tolerant species such as *Juncus kraussii, Lobelia alata, Gahnia filum* and *Schoenus nitens.* Where there are no burrows, the vegetation consists of dry or wet heaths dominated by *Banksia marginata* together with Epacridaceae such as *Epacris impressa, E. lanuginosa* and *Sprengelia incarnata*, Fabaceae (*Aotus ericoides, Pultenaea* spp., *Acacia* spp.) and Myrtaceae (*Leptospermum scoparium, L. glaucescens, L. lanigerum, Melaleuca squarrosa, M. gibbosa* and *M. squamea*). The heaths are the most species-rich communities at both locations. The vegetation grades through scrubs of *Leptospermum* spp. and *Melaleuca* spp. of low diversity to heathy woodlands dominated by *Eucalyptus viminalis* or *E. obliqua.* The structural and floristic variation in the vegetation is strongly conditioned by exposure, soil depth, fire and drainage.

Thus the halophytic communities develop on the most exposed coastal onshore areas, with the heaths occupying the deeper aeolian sands. *Melaleuca* and/or *Leptospermum* scrubs develop along drainage lines or small creeks, and the *Eucalyptus* woodlands are found on more sheltered sites on deeper soils. Frequent fires promote the heath vegetation at the expense of the scrubs. In the prolonged absence of fire, much of the heath containing the dominant *Leptospermum* or *Melaleuca* species would succeed to scrub, with a corresponding loss of species richness. On the other hand, too frequent fire promotes bracken. In the woodlands, infrequent fires result in a heathy or shrubby understorey. Very frequent, low-intensity fires result in bracken understoreys where the soils are sandy but tend to grassy understoreys where the overlying aeolian sands are shallow or where there has been admixing of the nutrient rich dolerite sub-soils and the sands.

The shearwater colonies are found on the deeper sands of the hinterland. Three main communities can be recognised:
(1) an open community of *Poa labillardieri/P. poiformis* and *Lomandra longifolia,* with considerable bare areas and a variable cover of introduced annual species such as *Bromus diandrus, Agropyron repens, Cirsium vulgare, Hordeum leporinum* and *Holcus lanatus*;
(2) a dense community dominated by *Pteridium esculentum,* with few other species present;
(3) a succulent halophytic herbfield community of variable cover but containing *Carpobrotus rossii, Tetragonia implexicoma,* and *Rhagodia baccata,* either in pure stands or in any combination.

These three communities represent different successional stages in the life of the rookery. The main determinants of the community present at any one site are degree of trampling and guano deposition, degree of incorporation of dead grass and other organic matter into the soil by the birds, and the effects of fire. The birds thus provide a strong biogenic control over the traditional successional pathways which are found in coastal areas where the birds are absent (e.g. Jackson 1968, Kirkpatrick 1977, Brown 1980, Brown & Podger 1982). The ordination by detrended correspondence analysis (DCA) of the Pineapples rookery is shown in figure 2. The encircled quadrats are the four major groups recognised in the Twinspan classification (see table 1). It can be seen from the ordination that the first axis aligns the sites from those with high DCA scores for the heath plots and no burrows, through intermediate values representing

TABLE 1
TWINSPAN analysis of Pineapples Rookery vegetation data

Vascular plant species	Burrow-rich sites, deep sandy soils	Coastal sites, shallow soils	Bracken-rich sites	Heath/scrub sites, no burrows	Twinspan divisions (3)
Acaena novae-zelandiae	---------------------	1-11---1	1------	----------	000
Juncus pallidus	---1-----------------	1----11-	--1----	----------	000
Leucopogon australis	---------------------	------1-	-------	----------	000
Lobelia alata	---------------------	11111111	1------	----------	000
Agrostis avenacea	---------------------	1-------	-------	----------	000
Apium prostratum	---------------------	1---1---	-------	----------	000
Baumea juncea	---------------------	11111---	-------	----------	000
Epilobium billardierianum	---------------------	1-------	-------	----------	000
Gahnia filum	---------------------	11-11---	-------	----------	000
Helichrysum reticulatum	---------------------	----1---	-------	----------	000
Juncus kraussii	---------------------	1-------	-------	----------	000
Oxalis corniculata	---------------------	1--1----	-------	----------	000
Rumex crispus	---------------------	1--1--1-	-------	----------	000
Stipa stipoides	---------------------	----1---	-------	----------	000
Veronica gracilis	---------------------	1-------	-------	----------	000
Sonchus megalocarpus	---------1----------1	--111---	-------	----------	000
Cirsium vulgare	--------11-----------	1-----1-	-------	----------	001
Scirpus nodosus	-----1---11111111--11	111---1-	-------	---1------	001
Bromus diandrus	----111111--1-1-11---	-------1	-------	----------	001
Carpobrotus rossii	1-1-111111111111-1---	11--1---	-------	----------	001
Holcus lanatus	----11---------------	--------	-------	----------	001
Hordeum murinum ssp. *leporinum*	-----11-1------------	--------	-------	----------	001
Solanum laciniatum	----------------111--	--------	-------	----------	001
Rhagodia baccata	11-1-----------------	--------	-------	----------	001
Tetragonia implexicoma	11-1----1--11111-----	1-------	-------	--1-------	001
Poa labillardieri	-1---1--111-11-111111	11111111	1-1----	------11--	001
Lomandra longifolia	111-1-1-------1111--1	1111--11	1---1-1	11-11111-1	010
Pteridium esculentum	1-11--1---1-111--111-	---1-111	1111111	11111111-1	010
Senecio vulgaris	1--------------------	--------	1------	----------	010
Dianella tasmanica	--11-----------------	---1-111	1---1--	-------1--	011
Leucopogon parviflorus	---------------------	-------1	1------	----------	011
Goodenia ovata	---------------------	-----11-	111----	-----111--	10
Melaleuca gibbosa	---------------------	----1--1	1------	-----1111-	10
Melaleuca squarrosa	---------------------	-----1--	111----	----1111--	10
Eucalyptus obliqua	---------------------	--------	------1	---1------	110
Hydrocotyle hirta	---------------------	--------	1------	----------	110
Leptospermum scoparium	---------------------	-------1	1-1----	--11111111	110
Olearia floribunda	---------------------	--------	------1	------11-1	110
Gahnia grandis	---------------------	--------	1------	-----1111-	111
Acacia myrtifolia	---------------------	--------	-------	---1111111	111
Acacia verticillata	---------------------	--------	-------	---1------	111
Amperea xiphoclada	---------------------	--------	-------	1---1111-1	111
Baumea acuta	---------------------	--------	-------	------1---	111
Allocasuarina monilifera	---------------------	--------	-------	-11-1111-1	111
Cassytha glabella	---------------------	--------	-------	----1-----	111
Epacris impressa	---------------------	--------	-------	----1111-1	111
Gonocarpus tetragynus	---------------------	--------	-------	-----11--1	111
Lepidosperma laterale	---------------------	------1-	-------	1--111111-	111
Leptocarpus tenax	---------------------	--------	-------	----111---	111
Olearia phlogopappa	---------------------	--------	-------	1---------	111
Pultenaea juniperina	---------------------	--------	-------	-------1--	111
Tetrarrhena distichophylla	---------------------	--------	-------	-----1-1-1	111
Banksia marginata	-1-------------------	--------	-------	1--11---11	111
Leptospermum glaucescens	---1-----------------	--------	-------	111------1	111
Helichrysum scorpioides	---------------------	--------	-------	------1-11	111
Lindsaea linearis	---------------------	--------	-------	----1---1-	111
Selaginella uliginosa	---------------------	--------	-------	-----1--11	111
Aira caryophyllea	---------------------	--------	-------	--------1-	111
Aotus ericoides	---------------------	--------	-------	---------1	111
Epacris lanuginosa	---------------------	--------	-------	--------1-	111
Gompholobium huegelii	---------------------	--------	-------	---------1	111
Gonocarpus teucrioides	---------------------	--------	-------	--------1-	111
Lagenifera stipitata	---------------------	--------	-------	---------1	111
Leucopogon collinus	---------------------	--------	-------	---------1	111
Opercularia varia	---------------------	--------	-------	---------1	111
Patersonia fragilis	---------------------	--------	-------	---------1	111
Pultenaea stricta	---------------------	--------	-------	--------11	111
Deyeuxia quadriseta	---------------------	--------	-------	---------1	111
Sprengelia incarnata	---------------------	--------	-------	--------11	111
Stylidium graminifolium	---------------------	--------	-------	---------1	111
Xanthosia pilosa	---------------------	--------	-------	--------11	111
Lepidosperma concavum	---------------------	--------	-------	---------1	111
Schoenus tenuissimus	---------------------	----1---	-------	-----1-111	111
Twinspan divisions, two levels	000000000000000000000 000000000000000000000	00000000 11111111	1111111 0000000	1111111111 1111111111	

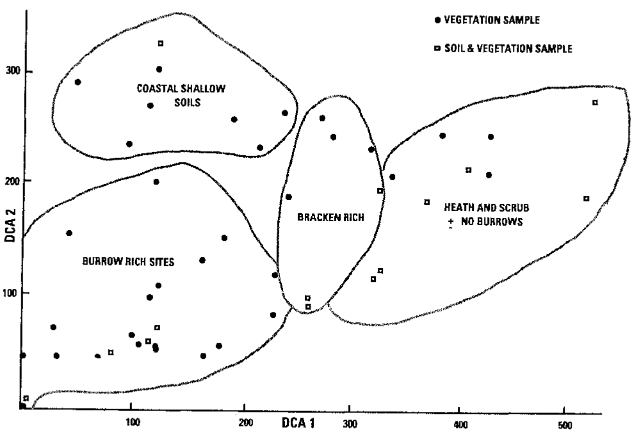

FIG. 2 — Ordination of sites at Pineapples rookery by Detrended Correspondence Analysis of their floristics. Sites where soils samples were taken are indicated.

scrub and woodland plots, again with few or no burrows, to sites with old burrows and thence to the lowest DCA score sites with high densities of currently active burrows. Some of the sites having low scores are very rocky, with only very shallow sandy soils. The second axis contrasts these shallow soil sites with the deep sandy sites of high burrow density.

Soil Nutrients

The complete soils data are given in table 2. The results of the factor analysis and varimax rotation are given in table 3.There are highly significant differences for nutrient status between the rookery and non-rookery sites at both locations, with elevated P and N concentrations to be found, as expected, on the sites of highest burrow density and/or bird activity ($F = 6.06$, $P < 0.05$ for phosphorus and $F = 7.07$, $P < 0.05$ for nitrogen).There were no significant interaction effects found in the ANOVA for P, but there was a highly significant site/burrow occurrence interaction

TABLE 2
Soil chemical analyses from Pineapples and Cape Deslacs rookeries

Site*	Burrows	pH	Conductivity TDS (mS)	Elements (ppm)					
				P	K	N	Ca	Mg	Na
1	+	4.6	0.40	014	120	3700	359	271	352
1	+	4.4	0.33	19	100	3000	381	171	180
1	–	4.2	0.24	14	60	400	454	223	168
1	+	4.6	0.18	45	80	1400	117	32	45
1	+	5.1	0.14	12	50	3000	201	101	130
1	+	4.5	0.23	140	80	3000	186	121	152
1	+	6.1	0.43	14	320	3400	311	394	518
1	+	5.0	0.94	53	310	4000	685	311	713
1	+	4.6	0.37	130	90	4500	274	91	112
1	+	4.7	0.38	28	90	1600	195	216	353
1	–	4.9	0.22	9	120	700	107	128	210
1	–	5.2	0.24	9	90	1100	242	465	287
1	–	4.9	0.16	5	80	800	81	210	170
1	–	4.9	0.09	6	50	1600	337	387	139
2	+	5.3	0.15	17	80	800	216	120	198
2	+	5.3	0.10	24	50	200	41	28	82
2	+	5.3	0.12	16	60	400	95	68	111
2	+	5.7	0.08	29	60	300	109	89	81
2	–	6.1	0.16	5	350	800	230	503	388
2	–	5.6	0.37	12	310	1100	628	223	352
2	+	5.3	0.16	9	30	200	56	58	87
2	+	5.5	0.25	6	140	700	158	159	314
2	+	5.4	0.15	13	50	400	150	125	106
2	+	6.1	0.04	1	40	200	65	64	46
2	+	5.7	0.10	56	60	600	201	64	96
2	+	5.7	0.22	48	70	900	333	165	184
2	–	6.0	0.26	5	220	700	471	310	527
2	–	6.1	0.22	6	300	900	438	384	410
2	–	6.2	0.28	8	380	1800	211	495	749
2	–	6.7	0.55	9	380	1400	681	365	710
2	–	6.1	0.23	7	130	500	196	121	247

* 1 — Pineapple; 2 — Cape Deslacs.

TABLE 3
Varimax rotated factor matrix of soil variables and ordination scores*

Variable	R.F.1	R.F.2
pH	**0.523**†	–0.058
TDS	**0.790**	0.435
log P	–0.102	**0.905**
log K	**0.789**	0.356
log N	0.316	**0.738**
log Ca	**0.644**	0.226
log Mg	**0.770**	–0.459
log Na	**0.940**	–0.064
DCA1	–0.260	**–0.920**
DCA2	0.457	**–0.583**

* Data from the Pineapples rookery
† Bold type indicates values greater than 0.5 irrespective of sign.

for N ($F = 32.36$, $P < 0.001$), reflecting the high variability of the soils at the Pineapples, where the differences between the high N concentrations in the bare areas and those of the heaths are very much more pronounced than in equivalent areas at Cape Deslacs, where no clear differences between burrow and non-burrow vegetation were apparent. That this trend is reflected in the vegetation composition is borne out clearly in the varimax rotation scores (table 3). Interestingly, the first factor reflects a saline influence, with Na, TDS, K, Mg and Ca being most highly weighted. Neither DCA axis is aligned strongly with this factor, suggesting that the major compositional trends in the vegetation are related to factors other than direct salinity effects, at least at this site, over the range of concentrations recorded. The direction of floristic variation may also be oblique to the direction of the salinity gradient. However, the second factor axis shows a very strong relationship between DCA 1, the major vegetation gradient, and a combination of N and P concentration, i.e. soil variables which relate directly to nutrient status. In fact, the second DCA axis grades the sites in order of soil depth, amount of organic matter incorporated in the soil (chiefly grass) and the density of burrows in combination. Thus it appears that, given the halophytic natures of the species involved, the succession of vegetation in the area is biogenically determined and does not reflect directly the usual underlying physical parameters, such as rock type, drainage or onshore effects of salinity. There is some evidence in the field of the residual vegetation which is so determined; e.g. the TWINSPAN analysis separates the group of *Melaleuca* spp. characteristic of poorly drained sites.

DISCUSSION

The vegetation of shearwater rookery sites is subject to stresses additional to those offered elsewhere in coastal environments. Surface-nesting birds, such as albatross and cormorants, give rise to considerable trampling and, of course, high levels of guano deposition. Guano is rich in phosphorus and nitrogen to the extent that it can be phytotoxic, especially in regions subject to drought (Gillham 1960). The vegetation in nesting areas of burrowing birds is prone to disturbances similar to those caused by surface-nesting birds but the burrows are usually (and necessarily!) located in areas of deeper soil development. Here, the use of sites is dependent on depth and friability of soils and on the likelihood of the burrow sites remaining free from inundation by water or from structural collapse, for the duration of use.

The shearwaters alter the habitat in the same way as surface-nesting birds by guano deposition and by trampling (especially in marshalling areas), but they also redistribute and incorporate surface organic matter into the soil, and they increase the degree of aeration of the soil volume.

The mechanical damage caused by the birds can lead to soil compaction ("hard ground") and also to pedestalisation of *Poa* tussocks. The bare areas are eventually colonised by *Tetragonia* and *Carpobrotus* after abandonment by the birds or through leaching of excess nutrients within the soil profile. These bare areas are often initially very nutrient rich and, in areas where a source of seed is available, they will support a flush of growth of exotic winter annuals such as *Avena, Hordeum* and *Bromus* spp., together with thistles and other Asteraceae. Such species are able to utilise the nutrients during the wet months and have set seed and died back by summer, when the likelihood of drought and nutrient toxicity becomes a problem for the less aggressive perennial native species.

Gillham (1965) considered that fire constituted a major cause of rookery depletion and cited altered levels of soil organic content in previously occupied sites after fire as evidence of this effect. Similar areas of "hard ground" were observed in parts of the present study areas and also, more extensively, in the commercial rookery areas on Great Dog Island (MJB, pers. obs.). The intensity and frequency of burning are known to be responsible for organic matter depletion in other Tasmanian ecosystems (e.g. Bowman *et al.* 1986). Fires may also kill the birds directly or cause abandonment of the sites, and may subsequently result in collapse of the system, since it is the birds which are responsible for the organic matter incorporation in the first place.

Thus, the succession in the rookery sites studied is strongly under the control of the birds themselves, but there is a pronounced effect also from human sources especially via fire or introduced weeds, as well as direct exploitation and physical destruction of burrows.

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